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TEXTBOOK OF GENERAL BIOLOGY

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TEXTBOOK OF GENERAL BIOLOGY

BY

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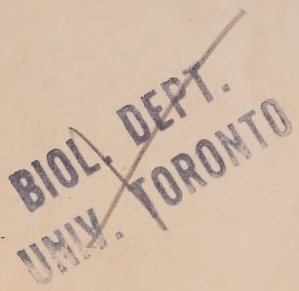

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THIS BOOK IS DEDICATED
TO MY FRIENDS
DONALD AND STELLA KEYES

PREFACE

This book has been written because of a feeling that there is a place for a fresh survey of modern Biology especially designed for those who do not plan to specialize in Botany or Zoölogy. Biology, as the term is used in this book, refers to those phenomena of life which are common to both plants and animals. No attempt is made to cover the fields of Botany and Zoölogy even in outline form, but rather to select from the wealth of illustrative material offered by each, such facts and theories as have a general significance. Such a selective process must necessarily be a subjective one, and the author recognizes his sins of omission and commission. But in a textbook designed for a course of one semester, or two terms, he can hope to present only an outline of biological principles arranged in what he considers a logical series.

Teachers are familiar with the difficulties encountered by students who attempt to wrestle with biological theories before they have some acquaintance with biological facts. Accordingly, since the average college freshman has had little science and less Biology, he is introduced to the subject by an account of the structure and activities of a vertebrate, the frog. Among the many desirable characteristics of this well-known martyr of the laboratory is the ease with which it may be compared with the human body, a real advantage to the beginning student. Following this an account of a flowering plant is provided. For this purpose the familiar wheat is chosen as an example of a highly organized and common plant. After describing the form, functions, and life history of this plant and comparing them with those of the frog, the student is ready to embark upon the study of general biological principles.

These principles seem to center about two concepts, that of the organism, and that of the species. The organism is distinguished by its ability to transform chemical substances, to respond to external stimuli, and to reproduce itself, and these properties are discussed in the light of modern biological research, from a physico-chemical standpoint. The species is considered as an aggregate of organisms distinguished by their hereditary

resemblances, their geographical distribution, and their descent from a common ancestor in evolution.

After a discussion of these principles a brief survey of the major plant and animal groups is intended to give some idea of the evolution of these kingdoms. Finally, a short account of some of the ways in which the study of Biology is applied to the improvement of human life concludes this introduction.

A frequent complaint arises that the beginning textbook in any science contains at least as large a vocabulary of unfamiliar words as the beginning text in a foreign language. While this may well be true, it is equally clear that these strange polysyllables are by no means a barbarous jargon designed to warn off all trespassers. On the contrary, they form a kind of scientific shorthand which is a real convenience to the professional scientist. The author has attempted to transcribe much of this biological stenography into plain English. Some of the symbols and abbreviations seem indispensable, but they have been reduced to a minimum and carefully defined. A pronouncing glossary is appended to the text.

It has been the author's aim to write for those to whom laboratory facilities are not available. Accordingly, illustrations have been used freely to take the place of demonstration material. These are carefully labeled, and the use of abbreviations has been avoided.

Biological principles are becoming increasingly important to the students of education, of psychology, and of the social sciences in general. These students, however, are so occupied with the immediate problems in their particular fields that they have little time for the technical vocabulary or the laboratory methods of another discipline. The author hopes that this book will prove serviceable to them and to the ever-widening circle of those who are trying to orient themselves in the world of modern science.

WALDO SHUMWAY

URBANA, ILLINOIS
March 21, 1931

ACKNOWLEDGMENTS

An elementary textbook in a science such as Biology, whose literature is so extensive and is increasing so rapidly, cannot hope to be original in more than arrangement and style. Nor can any writer of such a text pretend to have more than a speaking acquaintance with many of the subjects to be presented. His indebtedness to the original sources must be traced through one or more compilers who have preceded him. The present writer acknowledges his debt to his teachers, past and present, direct and indirect, and hopes that his present effort will not be unworthy of their teaching.

He is particularly grateful to his colleagues Professors H. B. Ward, Charles Zeleny, V. E. Shelford, and L. A. Adams of the Department of Zoölogy, to Professors C. F. Hottes and J. T. Buchholz of the Department of Botany, to Dr. W. A. McAllister of the Department of Psychology, and to Dr. D. H. Thompson of the Illinois State Natural History Survey, who have been kind enough to read chapters of this book in manuscript.

Full advantage has been taken of the generosity displayed by fellow authors and publishers in allowing the reprinting of illustrations from other texts. The usual acknowledgment is made in the legend of each figure borrowed from other sources; but the author's debt to Professors Holman and Robbins, who have generously permitted the reproduction of many figures from their textbook of General Botany, is particularly heavy. The original drawings have been prepared by the skilful hand of Mrs. Katharine Hill Paul.

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CHAPTER I

INTRODUCTION

The customary method of introducing the reader to a new subject is by means of a definition, such as "**Biology** is the science of life." A definition, however, is but a formal invitation to further acquaintanceship, and like many other formulae it is valuable only as it is used with discretion. If it were possible to tell in a single sentence all that Biology has come to mean, the reader might save his time by stopping at this point.

The Science of Life. — What is meant by the science of life? Without attempting to add another to the long list of formal definitions, let us say simply that we use the word science to mean "what we know about" a subject. And what do we know about life? That is a question man has asked since first he began to think. To primitive man life was associated with motion. In his myths and magic rites we find evidences of his belief in the animate nature of rock and stream, of wind and of rain. And though later speculation distinguished living plants and animals from all other objects of nature, the line of demarcation was not so sharp but that a belief in the origin of life from inanimate matter was quite as reasonable as in the obvious transformation of the living body into a lifeless mass. So, down the ages, those ancient mysteries of birth, the origin of life, and of death, its cessation, have challenged the attention of priest, philosopher, and scientist alike.

Content. — Plants and animals, to the best of our knowledge, are the only natural objects in which life is manifest. So Biology becomes the study of plants and animals. But the variety of life as it is expressed in a world of **organisms** (living things) is scarcely imaginable. Aristotle, "the father of Biology" (384–322 B.C.), was acquainted with some five hundred different **species** (kinds) of animals, while his pupil and co-worker Theophrastus (370–285 B.C.) described some five hundred plants. Two thousand years later Linnaeus (1707–1778) named about five thousand species of animals and approximately as many species of plants in the tenth edition of his "Systema Naturae"

(1758). He modestly estimated that the number of species described by him was less than half the number actually in existence. As a matter of fact a conservative calculation of the number of species described up to the present time gives us approximately a million species with a ratio of three animals to one plant.

Fig. 1. — Aristotle (384–322 B.C.), the father of Biology. (From Locy, "Main Currents of Zoölogy," Henry Holt and Co.)

Divisions. — In the university at Upsala, where Linnaeus taught, he was Professor of **Natural History,** a subject which included the animal, vegetable, and mineral kingdoms. Such a domain became too large and unwieldy, and now each kingdom is allotted to a separate science, **Zoölogy, Botany,** and **Geology** respectively. Lamarck (1744–1829), a great speculative zoölogist, recognized the essential similarity of plants and animals as living things and coined the word Biology[1] for the study of their common properties.

Fig. 2. — Theophrastus (370–285 B.C.), pupil and successor of Aristotle. Author of the first treatise on plants. (From Locy, "Growth of Biology," Henry Holt and Co.)

On the other hand, the detailed investigations of botanists and zoölogists resulted in the establishment of many special divisions of these sciences. This specialization has continued until the list of so-called biological sciences is too lengthy for enumeration at this point. It is well to note, however, that some, like **Bacteriology,** the study of bacteria, and **Entomology,** the study of insects, represent still further subdivision of Botany and Zoölogy, respectively. Others, like **Genetics,** which deals with the variation and inheritance of individual characteristics,

[1] Also used by Trevirano (1802).

collect their information from study of both plants and animals. The growing importance of these latter sciences emphasizes the fundamental unity of plant and animal life which is the proper field of **General Biology.**

The Organism. — The problems with which Biology deals center about the individual organism and the species, respectively. The organism demands our attention first, as it is in the organism alone that life is manifested. What is an organism? The word

FIG. 3. — Linnaeus (1707–1778), the founder of modern classification and nomenclature. (From Holman and Robbins, "A Textbook of General Botany," John Wiley and Sons, Inc.)

implies organization, or the arrangement of parts for particular purposes. Aristotle pointed out the dual aspects of the subject, the one dealing with the form (structure) of an object, the other dealing with its function (activity). Accordingly there have arisen two biological sciences known as **Morphology** and **Physiology,** respectively. The first deals with the question "How is the organism constructed?"; the other attempts to answer the query "How does it work?" The division is really a formal one, for the two sciences are interdependent, and each is incomplete without the other. In spite of the logical connection

between these two divisions, they were almost completely separated during the past century, principally because of a difference in method. The method of Morphology was primarily the description and comparison of observed forms and structures. The method of Physiology was primarily that of experimentation. This is but natural. The obvious way of studying a new organization is to examine its structural composition and to compare this with familiar organizations, but in order to see how it works the skeptical observer will try it on something new. The experimental ideal is to have all the conditions of the experiment so carefully controlled that it can be repeated under the identical conditions with the identical result. At the present time Morphology and Physiology are moving closer together, and each is applying the methods of the other school, as witnessed by the appearance of books on Experimental Morphology and Comparative Physiology. The study of the organism is incomplete without a knowledge of the way in which it came into existence. This is the province of the biological science known as **Embryology,** which deals with the origin and development of the individual organism. This subject is intimately related to both Morphology and Physiology, for the development of form and the development of function go hand in hand.

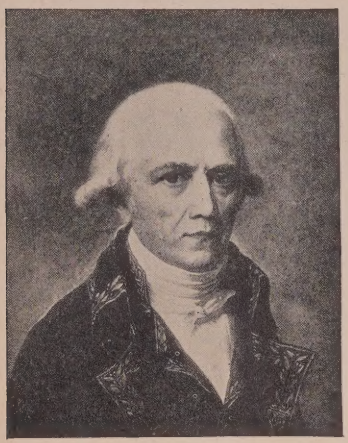

FIG. 4. — de Lamarck (1744–1829), an early evolutionary biologist, best known for his theory respecting the inheritance of acquired characteristics. (From Pirsson and Schuchert, "A Textbook of Geology," John Wiley and Sons, Inc.)

Physico-chemical Viewpoint. — The study of the individual organism is rapidly passing from the hands of the morphologist and physiologist into those of the chemist and physicist. Or rather the biologist is learning Chemistry and Physics. It was not so long ago that the term Organic Chemistry stood for a fancied distinction between the chemistry of the compounds found in the bodies of plants and animals, and other so-called inorganic substances. It is the fundamental postulate of modern

Biology that the structure and activity of the organism are subject to the same laws of Chemistry and Physics as are all other forms of matter and energy. Needless to say, the boundary between the inorganic world and the organic has not yet been crossed: living matter has not yet been built up from lifeless ingredients. But many organic substances have already been synthesized in the chemical laboratory, and the physicist has simulated many of the so-called vital phenomena. This physico-chemical interpretation of Biology (sometimes called the mechanistic conception of life) may not survive the test of long-continued experimentation and comparison, but it has already proved extremely fruitful and alone holds out hope for future investigation.

The Species. — Like produces like. The developing embryo gradually assumes the forms and functions characteristic of its parents. It is through this process of reproduction that the characteristics of the kind of plant or animal are transmitted from generation to generation. The species, then, is an aggregate of similar organisms presumably descended from a common ancestor. Linnaeus, who invented the modern system of naming and classifying plants and animals, employed the species as the smallest unit of his scheme. The species were arranged into **genera** (singular, **genus**), these into **families,**[2] and families into **orders.** Orders were grouped to form **classes,** and these were united into **phyla** (singular, **phylum**), or divisions of the plant or animal kingdom, as the case might be. With the enormous increase in the number of described species since the time of Linnaeus, the need for further subdivisions has been recognized in the creation of subspecies, subgenera, subfamilies, suborders, subclasses and subphyla. Some students of classification have even gone so far as to advocate superspecies, etc., to make the filing process more complete. Tables of classification are provided in the Appendix. It is to be remembered, however, that there is nothing sacred about these; they represent only a convenient method of pigeon-holing information so that it will be readily accessible, while the terminology concerned offers many memory-saving devices to the student of Latin and Greek, who may remember that **Spermatophyta** means seed plants and that **Insectivora** stands for insect-eaters.

Nomenclature. — In referring to plants and animals, Linnaeus invented what is known as the **binomial** system of nomenclature, in which the name of the genus (in the form of a Latin noun) is

[2] This group was not used by Linnaeus but was introduced by Batch (1780).

followed by the name of the species (as a qualifying adjective or the genitive case of a noun derived from the name of some person whom the describer wished to honor). Thus the name of the common leopard frog of Eastern North America is written *Rana pipiens*, as though we wrote the name of an individual as *Smith john*. There are supposed to be no duplications in the list of generic names, and no duplications of specific names within a given genus. In this way there is a sufficient number of combinations so that each kind of plant and animal may have a distinctive name. The use of the binomial does away with the ambiguities resulting from the use of the popular or vulgar name of an organism. Thus in America we speak of " corn " where the English use the term " maize," both meaning the plant *Zea mays*.

It must constantly be borne in mind that the species is not a natural but an arbitrary grouping. Many species contain more or less sharply defined subdivisions known as varieties or subspecies. The question then arises as to whether the subspecies should not be considered as independent species. The expert student in the group has his own ideas as to the relative importance of the various characteristics used for purposes of classification, and according to whether he is a " lumper " or a " splitter " there will be fewer or more species in the field of his specialty. Thus there appear to be two types of the American garden toad. The one specialist will call them *Bufo americana*, var. *americana*, and *Bufo americana*, var. *fowleri*; the next knows them as *Bufo americana* and *Bufo fowleri*.

Fig. 5. — Gregor Mendel (1822–1884), whose breeding experiments laid the foundation for modern Genetics. (From Curtis and Guthrie, "A Textbook of General Zoölogy," John Wiley and Sons, Inc.)

Problems of the Species. — With these finer distinctions of the professional **taxonomist,** as the expert in classification is called, we are not concerned. As long as there are different kinds of plants and animals we shall need names for them, and the Linnaean system of nomenclature still meets the immediate needs of the general biologist. But the existence of these different kinds of animals does present problems of particular interest. How do species maintain their

existence? How do they originate? The science of Genetics, which deals with the variation and inheritance of specific characters from generation to generation, dates only from the rediscovery in 1900 of the results obtained by the Abbot Gregor Mendel (1822–1884) in his monastery garden. **Ecology,** or the study of the relationships between species and the environment, is based on the concept of the biotic community, or assemblage of plants and animals, laid down in 1909 by Warming. The origin of species is the subject of **Evolution,** which Charles Darwin (1809–1882) made his own. Each of these biological sciences has its own methods of investigation and each has made contributions to our knowledge of the species, which, composed of innumerable individuals, past, present and future, and affected by the many factors of a changing environment, represents a temporary aspect of organic evolution.

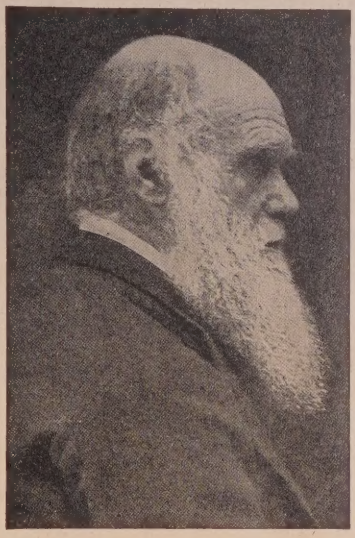

Fig. 6. — Charles Darwin (1809–1882), author of "The Origin of Species through Natural Selection." (From Pirsson and Schuchert.)

Applied Biology. — The application of the methods and principles of Biology has proven invaluable in many practical ways. In this general field of applied Biology, interest centers in research applicable to Medicine, Public Health, and Sanitation; to Agriculture which is concerned with the biological products of the soil and Aquiculture which deals with the biological products of the waters; to the conservation of natural resources, and other fields which will be indicated in the concluding chapter. But pure Biology, devoted to the acquisition of knowledge for its own sake, has its applications no less than has applied Biology. The theory of Evolution, for example, pervades the writings of psychologists, educators, and sociologists, and the philosopher who neglects the contributions of Biology is rare indeed.

CHAPTER II

A VERTEBRATE ANIMAL

Before commencing an examination of biological principles, it is necessary to gain some acquaintance with biological facts. The individual organisms with which Biology deals are either animals or plants, and these are the tangible units with which biologists work. Since we ourselves are animals and have some practical knowledge of our own bodies, it will be proper to commence our study with an account of an animal rather than of a plant, even though the structure of the plant is less complex. And because our own bodies are highly organized into specialized parts and regions, we select a highly organized animal, the frog, also a vertebrate animal, instead of a simpler and smaller, but more unfamiliar organism.

In the account that follows we shall examine the activities of the frog's body. These center around three main functions: **metabolism,** or the changes in chemical composition undergone by foreign substances taken in as food; **irritability,** or the transformations of energy manifested in the work done by the organism as it responds to external stimulation; and **reproduction,** or the ability to detach portions of the body which develop into replicas of the parent organism.

Throughout this discussion it must be borne in mind that we are dealing with the organism as a whole. Although we shall have to mention smaller units, such as **organs, tissues,** and **cells,** these exist in nature only as parts of the living organism, just as in chemistry atoms, the smallest units of the chemical elements, are naturally found combined in molecules, the smallest units into which chemical compounds can be subdivided and still retain their chemical properties.

THE FROG

This familiar animal has long played the martyr's rôle in the biological laboratory. Generally easy to obtain in numbers, convenient in size, clean and familiar, it affords exceptionally favorable material for dissection, experimentation, and field

observation. Although there are still many problems connected with the frog, so much has been learned from the study of this one species that it may well be considered a biological classic.

Species. — Nearly two hundred species of frogs, not including the toads and tree frogs, have been described, but the common frog in North America (excluding the Pacific coast) is the leopard frog, *Rana pipiens* (Fig. 7). These frogs appear in the early spring in our ponds, soon after the tree toads and peepers. In or near these ponds they may be found until late autumn, when they burrow in the mud to spend the winter in a condition resembling suspended animation which is known as hibernation.

Habitat. — If you approach the pond soon after the ice has melted you will hear a chorus of sounds among which may be distinguished the croaking of the leopard frog. As you draw nearer, the chorus dies down. A series of splashes indicates that the singers are taking to the water, diving deep and swimming beneath its surface. If you wait quietly you will see some swimming along with a stroke curiously reminiscent of the ancient breast stroke of our swimming schools, or floating easily with nostrils barely lifted above the water. Perhaps one may crawl out upon the bank and hop along the edge. Watch carefully and you will see some incautious insect suddenly disappear, snapped up by a lightning-like movement of the tongue. Specimens are easily captured while this congregation of frogs is assembled during the spring mating season, but when it is concluded they will disperse in all directions, each to take up a hermit's life.

FIG. 7. — *Rana pipiens*, the leopard frog. ½ natural size.

Shape of the Body. — If we catch a specimen, after a few frantic struggles to escape it will often lie quietly in the hand while a few observations are made. The body is bilaterally symmetrical, that is to say, right and left sides are practically mirror images of each other. We distinguish a head at the anterior end, but unlike most vertebrates the frog has no tail at the posterior end. The back (**dorsal** surface) is easily distinguished from the belly (**ventral** surface) not only by the difference in color and markings but by the fact that nostrils, eyes, and ear drums are located on the dorsal side.

Parts of the Body. — The parts of the body are the head, trunk, and appendages (arms and legs). The head of the frog, in which are to be noted the wide mouth, paired nostrils, protuberant eyeballs and prominent ear drums, is roughly triangular in shape and merges into the trunk without the intervention of a neck. The arms and legs, which terminate in webbed hands and feet, respectively, are jointed to form three segments, upper arm, forearm, and hand in the anterior appendage, which is the smaller; thigh, shank, and foot in the posterior appendage, which has been kicking vigorously.

Skin. — The skin of the frog is smooth, generally cool and slightly moist in the air owing to the presence of skin glands (Fig. 13). The secretion of these glands is, however, neither unpleasant nor harmful. The color, a light green on the dorsal surface and cream yellow on the ventral surface, is marked by large spots of dark green on head, trunk, and appendages.

Now if we do not have to take the frog back to the laboratory let us return him to his fellows and consider his daily activities. After the mating season, to which we will return in a later section, the adult frog spends his time in the capture of food, varied by brief periods of rest or sleep, and often by frantic attempts to escape from becoming the food of some predacious fish, reptile, bird or mammal, for the frog is considered excellent food by all, including man. Nor are the small frogs free from attacks by larger members of their own race.

FOOD AND METABOLISM

Insects, worms, and spiders form the main items in the dietary of the frog. But other forms of animal life about the same size are not overlooked, and cannibalism is not unknown. The adult frog is confined to a carnivorous diet; its food is composed of other animals' bodies. Some animals may obtain their food from plants, but none are able to build up their food from inorganic materials alone. In the human diet, whole animals and plants are seldom consumed. Selected portions are subjected to preparatory treatment by different methods and usually still further altered by cooking. A variety of foods is combined to secure a balanced ration. The frog, on the other hand, secures a ration balanced for the needs of its body mechanism by devouring its prey entire.

Nutrition. — Food may be considered in a sense the fuel of the body mechanism. The components are water, inorganic salts,

such as sodium chloride (common salt), and organic compounds. These are divided into three classes. **Carbohydrates** are the sugars and starches. **Lipins** include the fats, oils, and waxes. The **proteins** are complex nitrogen-containing compounds built up of smaller structural units called **amino-acids.** A further account of these compounds will be found in Chapter IV. The bodies of animals and plants contain these substances in varying amounts, and the animal diet requires a supply of all. In addition to these, recent investigations have disclosed the existence of a number of substances known as **vitamins,** the chemical composition of which is unknown, but which play an important rôle in nutrition.

A deficiency of vitamin A, found in the yellow fats (butter and cod-liver oil), and green leaves, may result in blindness. Vitamin B, found in green leaves, yeast, and seeds, is now thought to be made up of two substances, one of which is anti-neuritic, and the other anti-pellagric, i.e., its absence causes the disease known as beriberi. Vitamin C is found in the citrus fruits, tomato, and many salad vegetables. Its absence causes scurvy, the bane of the old-time sailing vessel. Vitamin D is anti-rachitic. Its absence causes a disease of children, known as rickets. It is found associated with vitamin A. A newly discovered vitamin E is concerned with the ability to produce offspring. It is found in the wheat seed and some green plants. Even frogs require vitamins, as tadpoles kept on a vitamin-free diet are smaller than the normal size.

Digestion. — The raw material taken into the body by frog or man undergoes a number of refining processes before it can be utilized further. These processes, which are in the nature of breaking down the complex chemical compounds of the food and making them soluble, are called as a whole digestion. The organs of the body which are concerned with these processes make up the digestive system (Fig. 8). In both frog and man, this system is in the form of a long and complicated tube through which the food is passed, its several components subjected to refining processes in different regions, the refined fractions absorbed, and the residue discarded.

Intake of Food. — The frog snaps up its prey by shooting out its tongue, which, unlike ours, is attached at the front end and free at the rear, and is covered with a sticky mucus secreted by its glands. The tongue is then drawn back and the food bolted into the **oesophagus,** a short and distensible canal leading to the stomach. The teeth of the frog are used only for holding the prey and not for grinding up the food in preparation for later

processes as in man. Nor are there salivary glands, as in man, which secrete a fluid to soften the food as it is chewed.

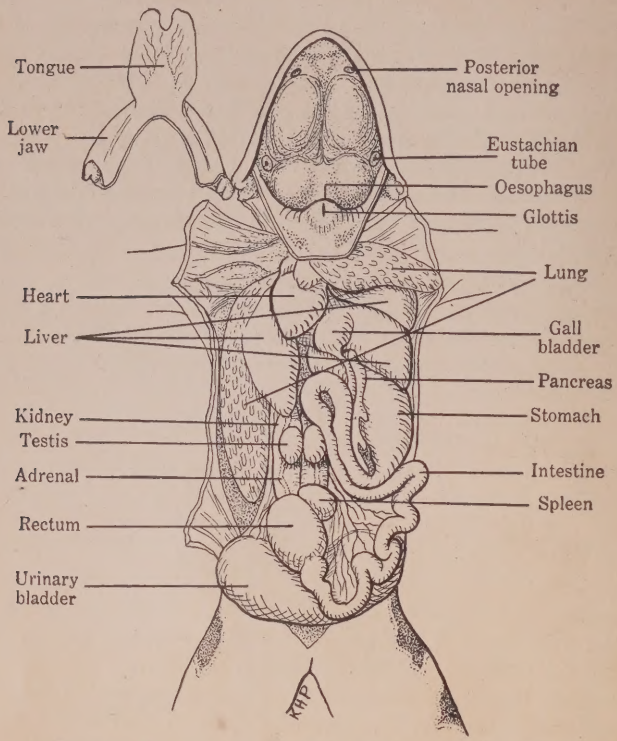

FIG. 8. — *Rana pipiens*, dissection from ventral side, $\times 1\frac{1}{2}$.

Digestive Tube. — Before examining the oesophagus and stomach further, let us examine a section (Fig. 9) across the digestive tube. Under the microscope we note that the innermost layer with which the food comes in contact is composed of bodies which are called cells. These are the smallest units with which we shall be concerned at this time. For the present we shall note them only as the structural units of the layers or other aggregates (tissues) which they make up. To return to the innermost layer, this is called the **mucosa,** and from its gland cells are poured out digestive fluids. By means of these fluids, different food substances are made soluble, or broken down to simpler compounds

which can be absorbed by the mucosa. The gland cells of the mucosa extend into a thin nourishing layer of cells called the **submucosa.**

Outside the submucosa we find a layer of muscles, mostly circular, by whose contractions waves pass down the digestive tube, so milking its contents along. Especially powerful muscles called **sphincters** are found at the points where one part of the system merges into another, to act as valves regulating the passage of the food. Longitudinal muscles, not found in the oesophagus, contract to narrow the tube at one point after another. In combination with the wave-like contractions of the circular muscles, these result in a thorough kneading of the contents against the mucosa, as the food passes down the tube.

Regions of Tube. — The oesophagus appears to be a direct continuation of the mouth cavity. Morphologists distinguish, between these, a region known as the **pharynx,** from which a narrow slit, the **glottis,** opens into the lungs. In man the oesophagus is but a connecting tube, but in the frog its walls are lined with glands, elongated tubular sacs, frequently branched, which prepare and discharge into the oesophagus chemical substances in whose presence the foodstuffs are broken down into simpler forms. These secretions contain **enzymes,** which act to speed up specific chemical reactions, a process which will be discussed later (page 90).

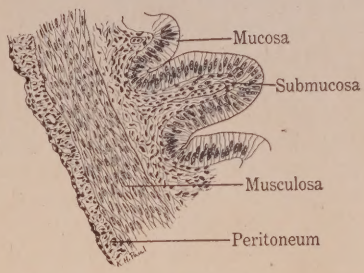

FIG. 9. — *Rana pipiens,* cross-section through part of the intestine, ×95.

The oesophagus passes imperceptibly into the stomach, which then widens gradually towards its posterior end where it unites with the small **intestine.** The wall of the stomach is muscular, and its mucosa is rich in digestive glands which secrete a variety of enzymes. These make up the gastric juice, which is quite acid on account of the presence of hydrochloric acid.

From the stomach the food is discharged into the small intestine, which is of smaller caliber than the stomach. Its anterior portion receives through a common duct the secretions of two greatly overgrown glands, the **pancreas** and the **liver.** These secretions together with the products discharged by many smaller glands compose the intestinal juice. The pancreatic

juice, which is alkaline owing to the presence of sodium carbonate, contains three main enzymes, which act on proteins, fats, and starches respectively. The bile, or juice of the liver, is alkaline also, but no enzymes have been identified. The foods are reduced by the action of the enzymes mentioned to water, inorganic salts, simple sugar (**glucose**), glycerine, and fatty acids, and the amino-acids of the proteins. In this form they are absorbed by the walls of the small intestine. The residues pass on into the large intestine, which is relatively short in the frog. In some herbivorous animals this is very large and contains a rich flora of microscopic plants called bacteria. These have the ability to break down the insoluble cell walls of plants into sugars which are absorbed by the mucosa of the large intestine. At the posterior end the large intestine narrows to become the **cloaca,** into which open the duct from the urinary bladder and the ducts of the genital organs. The contents of the cloaca are finally egested through the **vent.**

Nature of Digestion. — The digestive tube may be compared to a pipe-line down which raw materials are passed through, but not into, the body, subjected to various chemical and physical treatments at particular points, by which they are separated into valuable substances, which are filtered off, while the useless wastes and by-products are discharged at the other end of the tube. The physical treatment consists of the passage of the contents and the kneading against the walls of the tube. The chemical treatments involved are (1) the discharge (**secretion**) of enzymes by which part of the food is made soluble, and (2) the **absorption** of the soluble fraction into and through the mucosa. These processes are in a way the reverse of each other, for in secretion, materials pass from the mucosa into the tube, while in absorption, materials pass from the tube into the mucosa. The details of the process are left for later discussion (page 91).

A B

FIG. 10. — *Rana pipiens,* blood corpuscles; A, red; B, white, ×750.

Circulation. — From the mucosa the food, now in soluble form, passes into the blood vessels which lie in the next layer or submucosa. These vessels are a part of the circulatory system by means of which materials are transported from one part of the body to another. The actual carrier is the blood, which may be thought of as a fluid tissue composed of cells, the blood **corpuscles** (Fig. 10), and a fluid, the blood **plasma.** The

corpuscles are of two kinds, red and white. The former are strictly confined to the interior of the blood vessels, while the latter together with the blood plasma may escape through the walls of the blood vessels. New blood corpuscles are constantly being formed in such centers as the marrow of the bones, and old ones are being destroyed, for example, in the spleen and liver. The blood has well been termed " the common carrier of the body." Supplying all parts of the body, it maintains what has been expressively named " the internal environment."

Blood Vessels. — The vessels which make up the blood-vascular system lead towards or away from the heart. This is

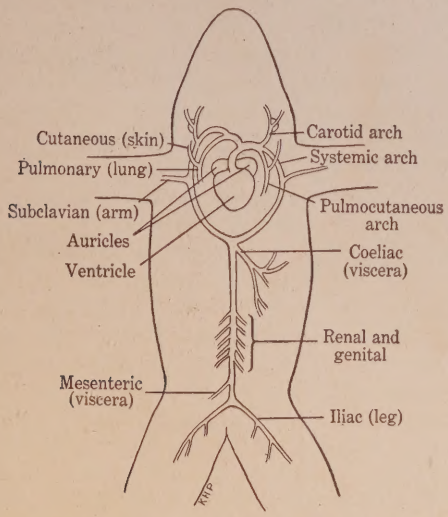

FIG. 11. — *Rana pipiens*, diagram to show principal arteries.

composed of three chambers, of which one is the **ventricle** or pumping chamber by which the blood leaves the heart, while the other two are **auricles** or receiving chambers. The walls of the ventricle are very muscular, and the rhythmic contraction of these muscles forces the blood forward into the **arteries** (Fig. 11), as the vessels which convey blood away from the heart are called. The general plan of the arterial system is as follows: from the ventricle a short tube, the ventral **aorta,** runs forward and divides into three branches, the **aortic arches,** on each side; the second pair of these curve up and around the pharynx and join

again to form the dorsal aorta, which runs back underneath the backbone. The first pair of aortic arches run forward into the head, while the third pair send branches to the lungs (**pulmonary** arteries) and to the skin (**cutaneous** arteries). All other parts of the body are supplied by branches from the dorsal aorta. The arteries terminate in very tiny branchlets, the **capillaries.** These capillaries soon reunite to form larger vessels called **veins** (Fig. 12), which convey the blood back to the heart. These veins are called the accompanying veins as they correspond to the

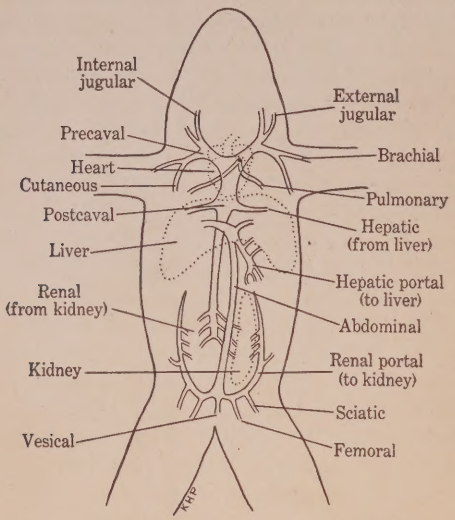

FIG. 12. — *Rana pipiens*, diagram to show principal veins.

final divisions of the arteries. The accompanying veins unite into larger trunks until there are three great vessels of the venous system entering the right auricle, namely, the right and left **precaval** veins from the head and arms, and the **postcaval** vein from trunk and legs. The blood from the lungs, however, enters the left auricle by means of the pulmonary veins.

Lymph Vessels. — In addition to the arteries and veins, the frog possesses an extensive lymphatic system consisting of irregular vessels and spaces in and between the tissues. Some of the spaces are quite large and serve as reservoirs. Others, with muscular walls, pulsate to force the **lymph,** which is composed of

blood plasma and white blood corpuscles, into lymphatic trunks and so back into the blood vascular circulation at junctures between the lymphatic trunks and the veins.

Food in Circulation. — The food absorbed by the mucosa of the intestine passes into the capillaries in the submucosa which unite to form the **hepatic** vein, by which they are carried to the liver, and thence, through the **hepato-portal** vein, to the heart. The fats, however, are taken into the lymphatics of the intestine and carried to the lymphatic trunk, which discharges into a vein running to the left precaval vein. In this way they pass immediately into the common circulation. In the liver the sugars are extracted in part from the capillaries and built up into **glycogen,** an insoluble substance sometimes known as animal starch. About half of the glycogen stored in the body is in the liver, while most of the remainder is to be found in the muscles. The glycogen stored in the liver is broken down again into soluble sugar and released into the blood stream when a sugar deficiency occurs. Fat is also stored in bulk in the connective tissues, particularly those underlying the skin, surrounding the viscera, or separating the muscles, which receive the general name **adipose** tissue. The simple proteins are not stored in bulk but circulate in the blood along with the simple sugars and fats, water and its soluble inorganic salts, while the individual cells extract the different substances in varying amounts by absorption.

Assimilation and Dissimilation. — In a later chapter we shall examine the activities of the cells concerned with the building up of more complex chemical compounds from these simpler constituents until they form a part of the very substance of the cell, **assimilation.** Here it is sufficient to say that these synthetic reactions require the expenditure of energy, and that this energy is supplied by the breaking down of the more complex substance of the cell into simpler chemical compounds, **dissimilation.**

Respiration. — Dissimilation may be compared very roughly with combustion or oxidation. When wood is burned a supply of oxygen is requisite, heat is produced, and the end-products are carbon dioxide, water, and ash. In the process a number of intermediate products are formed. So in the dissimilation of the body, oxygen is supplied and carbon dioxide is given off by the respiratory organs, water and substances in solution are disposed of through the kidneys and their ducts (see **excretion,** page 19), while the blood acts as a common carrier throughout.

The Lungs. — The adult frog respires by means of the lungs, skin, and the mucous lining of the mouth and pharynx. In man the lungs are contained in a separate cavity of the body known as the **pleural** cavity, which is contracted or enlarged through the action of a muscular sheet called the **diaphragm.** In the frog, on the other hand, the lungs (Fig. 8) lie in the general body cavity, the **coelom,** and the air is pumped in by the action of muscles in the floor of the mouth. The air in the mouth and pharynx is changed by raising and lowering the floor of the mouth while the nostrils are open and the glottis is closed. A certain amount of respiration takes place in the mouth and pharynx during this period. Then the nostrils are closed, the glottis opened, and as the floor of the mouth rises, air is forced into the lungs. This is known as inspiration. The reverse action, expiration, is accomplished by the contraction of the body wall muscles aided by the contraction of the muscles in the walls of the lung itself. The inner surface of the lungs is divided by a series of small partitions into tiny chambers which greatly increase the area exposed to the air contained. It has been calculated that the total area of exposed surface of the lungs is roughly two-thirds as large as that of the skin. Next to the lining layer of the lungs come the capillaries which connect the pulmonary arteries with the pulmonary veins.

Lung Breathing. — The blood carried by the pulmonary arteries has come by way of the third aortic arch from the right auricle and is rich in carbon dioxide. In the thin moist layer lining the lungs, the carbon dioxide is given off and oxygen absorbed. The nature of this gaseous interchange will be considered as a cellular activity in a later chapter (page 91). In the blood stream the oxygen enters into an unstable combination with an iron compound, **haemoglobin,** in the red blood corpuscles. From the capillaries the blood stream enters the pulmonary veins, which convey it to the left auricle. After passing through the ventricle, this blood is diverted into the first and second aortic arches and so to all parts of the body.

Skin Breathing. — In cutaneous as opposed to pulmonary respiration, the skin functions either in or out of water, and during the period of hibernation, carries on practically all of the respiratory activity. The skin has two layers (Fig. 13), an outer **epidermis** and an inner **dermis,** the dermis being rich in lymph spaces and blood capillaries. The epidermis contains many glands whose function is to secrete the mucus by means of which

the skin remains smooth and moist. The respiratory exchange takes place in the epidermis, by means of the capillaries of the dermis, to which blood laden with carbon dioxide comes by way of the cutaneous arteries, and from which the cutaneous veins convey the oxygenated blood to the precaval veins. The lining of the mouth and pharynx is also supplied by the cutaneous arteries.

Internal Respiration. — The exchange of gases between the blood stream and the atmosphere is sometimes called external respiration, while the exchange between the blood stream and the parts of the body is termed internal respiration. This, like ex-

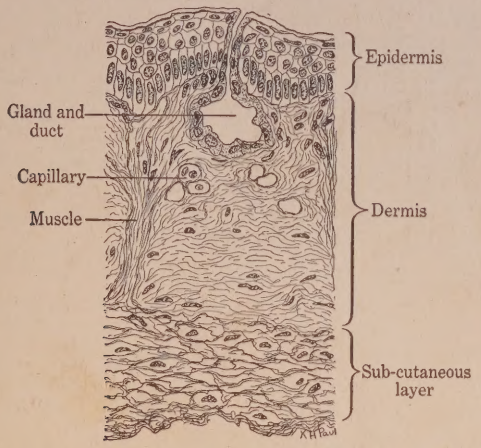

FIG. 13. — *Rana pipiens*, section through skin, ×200.

ternal respiration, is essentially a cellular process and will be discussed as such later. Meantime we note that the oxidation for which the oxygen is supplied by the respiratory process takes place within the separate cells, and that the carbon dioxide is but one of the end-products of intracellular dissimilation.

Excretion. — The end-products referred to above are carbon dioxide, water, nitrogenous wastes of protein dissimilation, and inorganic salts. These the animal cell is unable to assimilate and consequently discharges into the blood to be carried to organs especially concerned with their disposal. The nitrogenous waste excreted by the cells is in the form of ammonia but is changed in the liver to **urea,** a soluble salt, and is carried to the kidneys in this form.

The Kidney. — The **kidneys** of the frog (Fig. 8), found on the dorsal side of the body cavity, are two large complex glands, each composed of a great number of coiled tubules emptying into a duct called the **ureter.** These ducts convey the products of the tubules into the urinary **bladder.** The tubules of the kidney start as hollow capsules indented by the in-pushing of a knot of capillaries known as a **glomerulus** (Fig. 14). This knot is formed by the subdivision of a small artery, which with its fellows was derived from the dorsal aorta by way of the **renal** arteries. From the glomerulus the artery emerges and breaks up into capillaries which unite to form a small vein. This unites with others to

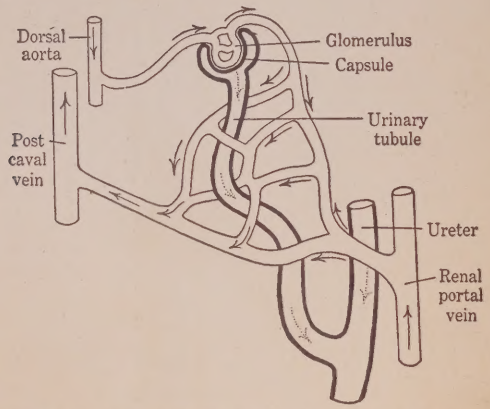

FIG. 14. — Diagram to show relationships of the capillaries of the kidney to the urinary tubule. The arrows show the direction of circulation. (After Curtis and Guthrie.)

form the renal veins which empty into the postcaval vein. The glomerulus is completely surrounded by the capsule except at the point where the capillaries enter and emerge. The capsule continues as the secretory portion of the urinary tubule, around which are entwined capillaries derived in part from branches of the renal arteries but mainly from those of the **renal-portal** vein which conveys blood from the posterior region of the body. The distinctive functions of the capillary networks have not been sufficiently investigated, but it is established that in the capsule and secretory portion of the tubule, water, urea, and other salts are absorbed from the capillaries and washed out into the ureter and thus conveyed to the urinary bladder.

In the frog, the tubules of the kidney become closely associated with the male genital gland or testis. An account of this association is postponed until a later section (page 39).

The Bladder. — The urinary bladder (Fig. 8) is a thin-walled sac, very distensible, with a network of muscle fibers; it opens into the cloaca just below the openings of the ureters. As the opening into the cloaca is generally closed by a sphincter muscle, the urine accumulating from the ducts collects in the bladder. This later expels its contents by the contraction of the muscles in its walls. The urine discharged from the bladder in twenty-four hours may exceed the total weight of the frog, for this animal is in no need of conserving water, owing to the large amount absorbed through the skin. It is stated that the reverse process, the secretion of water from the skin, may involve a certain amount of excretion, but there is no satisfactory evidence on this point.

The Endocrines. — The blood not only serves as a common carrier for the products of digestion, respiration and excretion but also conveys through the body the products of certain ductless glands which discharge their secretions directly into the capillaries. These secretions or **endocrines** stimulate reactions in parts of the body often quite remote from those in which they are formed and are for that reason sometimes called **hormones** or chemical messengers. Many of the organs which were formerly considered merely the vestiges of ancient structures and quite functionless, are now recognized as important endocrine glands. Among these are the **thyreoid,** the **parathyreoids,** and the **thymus,** which lie in the neck region; the **adrenals,** which are near the kidneys; the **pituitary** (Fig. 18), arising from the base of the brain, and the **pineal** from its roof. In the limits of this text, we must restrict ourselves to a brief statement concerning the activities of the thyreoid gland. This gland secretes an iodine-containing compound known as **thyroxin,** which in amphibia is concerned with the metamorphosis of the tadpole into the adult frog. If this substance is withheld by the removal of the thyreoid, the tadpole fails to become adult. If, on the other hand, the amount in the blood stream is increased by feeding or injecting thyroxin or grafting bits of living thyreoid tissue, the speed of metamorphosis is greatly accelerated.

Many of the glands provided with ducts elaborate endocrines as well. Thus the wall of the small intestine, while contributing enzymes into the intestinal juice, also forms an endocrine called

secretin which passes through the blood stream to the pancreas, where it stimulates that gland to the secretion of the pancreatic juice. So, too, the pancreas elaborates an endocrine called **insulin** which regulates the amount of sugar present in the blood.

The term endocrine balance is used to refer to the effects produced by the various endocrines on the general activities of the body and to the theory that an overproduction or underproduction of even one of these may lead to a disharmony, with serious if not fatal results.

Metabolism. — In the foregoing account of digestion, circulation, respiration, excretion and endocrine production we have been dealing with the chemical changes which take place in the body of the frog, largely in connection with the introduction of food and its subsequent history. All these as well as other chemical changes to be mentioned in the following sections make up what is known as metabolism, a phenomenon characteristic of all organisms. It will be considered at greater length in Chapter IV.

WORK AND IRRITABILITY

Chemical reactions involve parallel transformations of energy. So the processes of metabolism in the frog result in the transformation of energy of position (potential energy) into energy of action (kinetic energy) manifested as work, heat, chemical energy, electrical energy, and sometimes as light. Part of the energy so transformed (chemical energy) is utilized in the chemical reactions of metabolism, but the remainder is available for those movements of the body which serve to distinguish the animal from the plant. A large part of this energy is dissipated as heat.

There have been mentioned already certain movements of the digestive tube, heart, lungs, and bladder, but in contrast to these so-called visceral activities, we now have to deal with movements which involve the leverage of bones and may therefore be called skeletal movements. These latter are brought about in response to stimuli, or changes in the environment. We shall see in Chapter V that this property of responding to stimuli is characteristic of all organisms and is known as irritability.

The Skeleton. — The skeleton of the frog is essentially a connective tissue modified in regions of greater stress by conversion into **cartilage** or into bone. Cartilage, or gristle, is a clear semi-transparent and semi-rigid tissue covered by a membrane, the **perichondrium.** It is sometimes calcified by the

deposition of calcium salts. Bone is the most rigid tissue of the body because of its heavy impregnation by lime salts, which make up more than half the bone by weight. The bones are covered by a layer of **periosteum.** Both perichondreum and periosteum give rise to new cartilage or bone cells by means of which these tissues continue growth. The long bones are hollow and contain the bone marrow in which new blood corpuscles are formed.

The bones because of their hardness persist long after the death of the animal. Indeed, if favorable conditions exist they become petrified and, as fossils, give evidence of the structures of animals long since extinct. Their study therefore is most important in morphology, and as a result much is known about the form of bones.

Less attention has been paid to their functions. It is of course natural to think of bones as the supporting framework of the body, and the very word skeleton has been carried over into every-day language to convey this idea, as when we speak of the steel skeleton of a skyscraper. But when we think of the animal as a working mechanism, it is clear that the members of the skeleton are not only struts and ties but also levers for the movements of the body.

Parts of the Skeleton. — All told there are 158 bones in the skeleton (Fig. 15) of the frog, many of which differ from each other only in that the one on the right side is the mirror image of the one on the left. The separate bones are associated with each other in functional groups and are often bound together by ligaments, united by cartilage, or fused with each other in a bony union. Two major divisions are distinguished, the **axial** skeleton, including the bones of the head and trunk, and the **appendicular** skeleton of the arms and legs.

The Bones of the Hindleg. — Let us look first at the bones of the powerful hindleg used in leaping and swimming. This group is attached to the backbone by the **pelvis,** a Y-shaped bone formed by the fusion of three elements about a cup-shaped depression. Into this depression fits the head of the long thigh bone, thus making a ball and socket joint. At the further end of the thigh bone (**femur**) is an equally long shin bone (**tibio-fibula**) formed by the fusion of two parallel bones comparable to the **tibia** and **fibula** of the human skeleton. This is succeeded by the ankle bone in which two separate **tarsal** elements corresponding to the **tibiale** and **fibulare** of human anatomy have fused at each end, thus giving the foot additional length. The foot itself is

composed of a very short sole, with two bones representing the five **metatarsals** of the human foot, and the elongate bones (**phalanges**) of the five toes, each with from three to five separate bones. Internal to the first or big toe are the two short bones of the **prehallux,** an accessory toe which widens the web of the foot.

The Femur. — A closer examination of the femur shows that this bone has the form of a curved lever, the head end forming

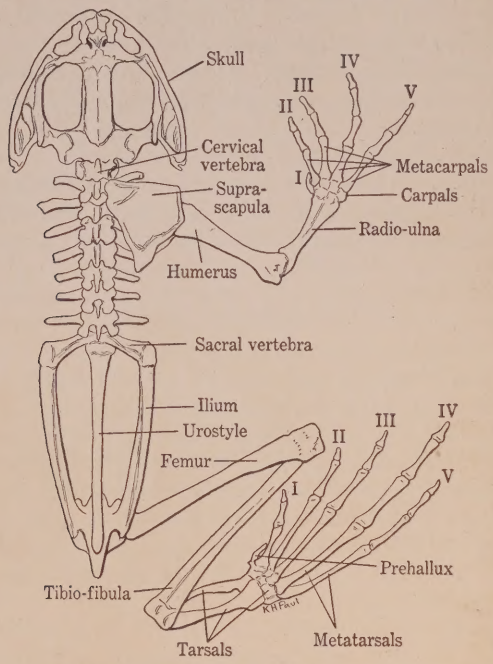

Fig. 15. — *Rana pipiens,* skeleton. From a dried preparation, ×1.

part of a ball and socket joint with the pelvis while the lower end makes a hinge joint with the tibio-fibula. At these articulating surfaces the bone is cartilaginous; elsewhere it is thoroughly ossified. The shape of the bone in cross-section is circular. In the center, where the greatest strains occur, the walls are thickened.

The structure of the bone is not a solid one but a honeycomb arrangement of microscopic bridges or stress lines called **trabecu-**

lae, which form struts and ties conforming to the tension and compression involved in the leverage of the bone. The cartilaginous ends of the bone afford a measure of adaptability to changes in shape because of their elasticity. They also serve as a buffer to take up the shock between bones when these are acting as a compound lever. As cartilage rubs against cartilage some of the cartilage cells are destroyed and form a lubricating film between the two articulating surfaces. As this lubricant, the **synovial** fluid, is destroyed, it drains out of the capsule of connective tissue surrounding the joint into the blood vessels with which the joint is provided, while new cartilage cells are broken up to form a new supply of lubricant. The bone, it must be remembered, is a part of the living body just as much as any of the softer parts heretofore discussed, and a moment's reflection on the changes involved in growth or in repair following the breaking of a bone will bring a realization of the extreme plasticity of bone architecture.

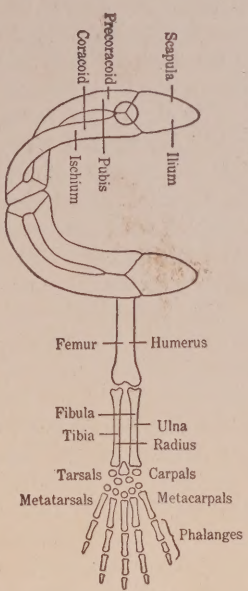

FIG. 16. — Diagram to show serial homology between the bones of the arm and leg. Shoulder bones above, pelvic bones below. Arm bones to right, leg bones to left. (After Kingsley, from Shumway, "Vertebrate Embryology," John Wiley and Sons, Inc.)

The Foreleg. — The foreleg or arm is not so well developed in the frog as the hindleg. Nevertheless it is built upon the same plan, and the accompanying figure (Fig. 16) shows that it contains bony elements corresponding to those of the hindleg. Such a correspondence of structure in two succeeding parts of the body is called serial **homology.**

The Backbone. — The backbone is a succession of serially homologous bones which make up a flexible supporting axis for the vertebrate body. Each **vertebra** has an arch on the dorsal side through which the spiral cord of the nervous system passes. The hindleg is firmly attached to the vertebral column by its girdle. The girdle of the arm is bound to the column in a more flexible manner, and is united with the breast bone or **sternum.** There are no ribs in the frog skeleton.

The Skull. — At the anterior end of the vertebral column is found the skull, which forms a protective covering around the brain and sense organs of the head and includes the upper and lower jaws. These are levers by means of which the mouth is opened and closed. The skull has a limited range of movement (articulation) upon the vertebral column, the anterior element of which (the cervical vertebra) is modified in structure, but there is no neck or neck vertebrae such as are found in the human skeleton.

The skull is a complex of many elements, some of which are cartilaginous but most of which are separate bones. The study and comparison of these elements in the skulls of living and extinct vertebrates is one of the famous lines of zoölogical research in which such men as Goethe, Huxley and many others interested themselves, but one to which the limits of this text will allow no further space.

The Muscles. — The movements of the bony levers upon their fulcra are caused by the contraction of the **skeletal** muscles, which altogether make up the flesh of the frog, by weight the greatest part of the body. These are not the only muscles of the body, for, as we have noted above, there are others which cause the movements of the digestive tube, lungs, etc., and which are known collectively as the **visceral** muscles. The skeletal muscles are made up of individual elongate muscle fibers which reveal under the microscope numerous tiny cross striations, on account of which this type of muscle is often known as striate or striped muscle. The visceral muscles do not have these striae, and for that reason are called smooth muscles. The skeletal muscles are sometimes called voluntary muscles because of their control through the central nervous system, while the visceral muscles are termed involuntary because the **autonomic** (**sympathetic**) nervous system governs their activity. It is maintained by some that there is no fundamental difference between these groups and that the distinction is merely one of degree. The skeletal muscles, it is said, perform relatively rapid movements, involving high tensions, and under complete central control, while the visceral muscles carry on slow movements with low tensions and are generally automatic. The heart is a unique example of an intermediate type, as its fibers are striated but its action is involuntary (see also page 110).

Metabolism of Muscles. — The twitch of an isolated skeletal muscle consumes about the tenth part of a second and includes a

latent period of about .01 second, a contraction period of about .04 second and a relaxation period of about .05 second. It appears that following the stimulation of the muscle, glycogen, which is stored in the muscles as well as in the liver, is converted into lactic acid. It is believed that the acid acts on the contractile fibers to bring about the contraction period. After this the acid is neutralized, bringing on the relaxation period. During this period the lactic acid is again converted into glycogen, the necessary energy being obtained by the combustion of about one-quarter of the lactic acid present. In this oxidation a perceptible amount of heat is liberated, oxygen consumed, and carbon dioxide and water formed.

Heat Formation. — It has been shown that the efficiency of the contraction phase is practically 100 per cent, as all the tension developed can be used for work. But for the entire cycle the efficiency is only about 50 per cent, since part of the energy as we have seen is used as heat of combustion. In cold-blooded animals like the frog, this heat is rapidly dissipated through the blood stream to the skin, and the body heat of the frog is seldom more than a degree above that of the surrounding water or air. In warm-blooded animals like man, however, there exists a mechanism for the regulation of body temperature. The production of heat is increased by muscular activity or decreased by rest. The loss of heat at the surface may be increased by the dilation of the surface capillaries or decreased by their contraction. The temperature is also affected by changes in the amount of water secreted by the sweat glands of the skin and the consequent increase or decrease in the amount of evaporation. Insulating coats such as the feathers of birds or the hair of mammals are also effective in the retention of heat.

Skeletal Connections. — The skeletal muscles, as their name implies, are attached to the bones directly or by means of bands of tough connective tissue called **tendons,** formed by the continuation and thickening of the connective tissue sheaths surrounding the muscle. The end of a muscle attached to a relatively immovable part of the skeleton is called the **origin,** while the other end attached to the more movable bone is known as the **insertion.**

Muscles of the Leg. — Anatomists say that over 150 different skeletal muscles are distinguished in the frog. We will examine the action of some of those of the leg (Fig. 17). These are in general arranged in antagonistic pairs. An **adductor** muscle

pulls the limb towards the mid line; an **abductor** pulls it away from the mid line. An **extensor** muscle straightens the limb; a **flexor** bends it upon itself. **Rotators,** found only in connection with ball and socket joints, cause the femur, for example, to rotate in the socket of the pelvis. **Levators** raise the attached bone; **depressors** lower it. Table I shows the relationships.

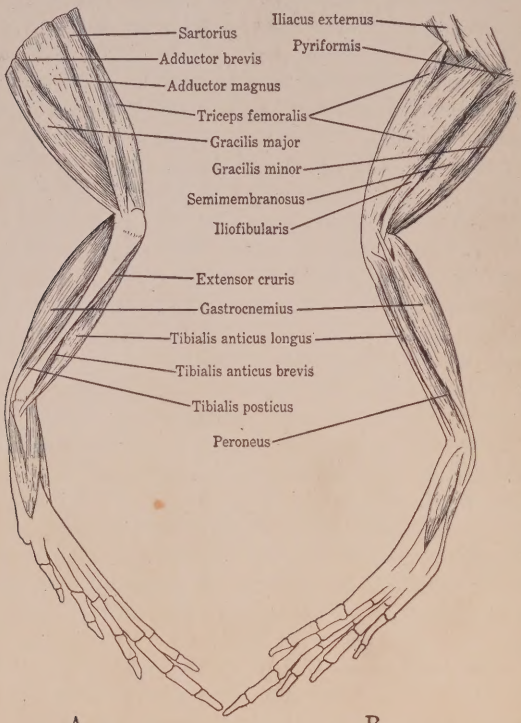

FIG. 17. — *Rana pipiens*, muscles of left leg; A, from below, B, from above, ×1.

The Nerves. — The contraction of the muscle fibers is in response to the stimulation produced by the discharge of a nervous impulse. The nature of the impulse has not been conclusively demonstrated, but it appears to be an electric current, transmitted through a highly specialized nerve element or **neurone.** Each neurone has an elongate process called the **axon** at one end, and small branching processes, the **dendrites,** at the other. Some

of these neurones attain great lengths, a meter in the human leg, for example. The axon or nerve fiber is generally encased in a **myelin** sheath which may be insulating in nature, but where it

TABLE I

MUSCLES OF THE FROG'S LEG ARRANGED ACCORDING TO FUNCTION

Origin: pelvis	Insertion: femur
Adductor magnus	Depresses thigh. Acts as abductor if head of femur is already in front of line connecting origin and insertion of this muscle. Otherwise as adductor.
[1] Adductor longus	Depresses and abducts thigh.
Adductor brevis	Same as a. longus.
Pyriformis	Levates thigh.
Iliacus externus	Rotates femur forward.
[1] Iliacus internus	Abducts thigh.
Origin: pelvis	**Insertion: tibio-fibula**
Sartorius	Abducts and depresses thigh; flexes shank.
Triceps femoralis	Abducts thigh; extends shank.
Gracilis major	Adducts thigh: flexes shank if at less than 90° angle to thigh; extends shank if at more than 90° angle to thigh.
Gracilis minor	Same as g. major.
Semimembranosus	Same as g. major
Ilio-fibularis	Levates thigh; flexes shank.
[1] Semitendinosus	Adducts thigh; flexes shank.
Origin: femur	**Insertion: tibiale-fibulare**
Gastrocnemius	Flexes shank; extends foot.
Tibialis posticus	Extends foot if flexed; flexes it if extended.
Tibialis anticus longus	Extends shank; flexes foot.
Extensor cruris	Extends shank.
Tibialis anticus brevis	Flexes foot.
Peroneus	Extends shank; extends the foot if partly extended, flexes it if partly flexed.

[1] Not shown in dissection (Fig. 17).

discharges to the muscle fiber, the **neuromuscular** junction (Fig. 81), the branching processes are not covered by this sheath. If we trace back the nerve fibers from the muscle which they supply, we find all those supplying a particular muscle uniting to form a nerve, and further all those from a particular region joining again, cable-like, until they unite in a central nervous system.

Central Nervous System. — This central nervous system (Fig. 18) is a hollow tube extending the length of the body, with an

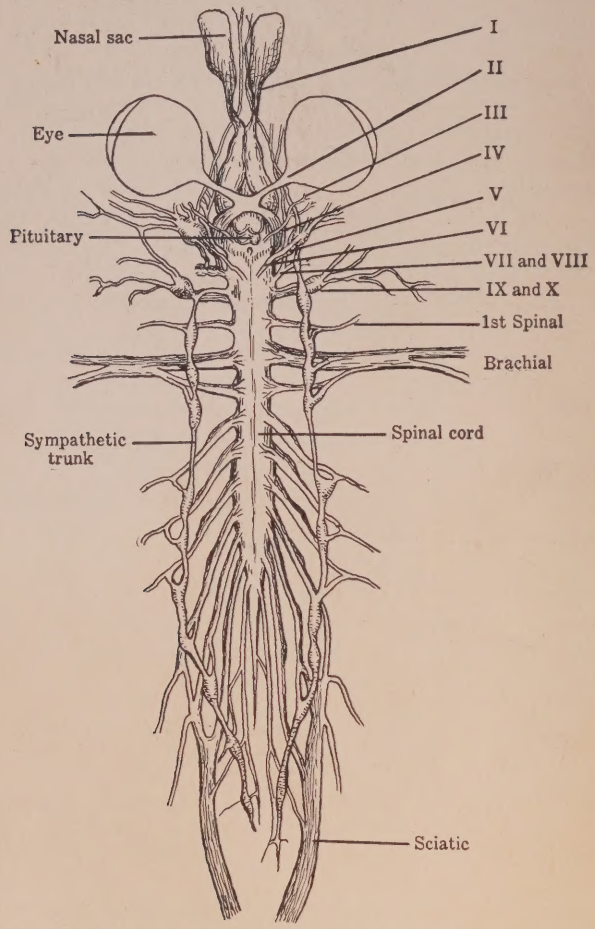

FIG. 18. — *Rana pipiens*, central nervous system from the ventral side, showing the origin of the cranial (Roman numerals) and spinal nerves, together with the nasal sacs and eyes. Somewhat schematic. ×2.

enlarged portion in the head called the brain, in distinction to the remainder of the tube which is known as the spinal cord. A

section across the cord (Fig. 19) reveals three layers, an inner layer which lines the central canal, a middle gray layer containing the cell bodies of the neurones, and an outer white layer made up of their myelinated axons. If the section passes through the point where one of the ten pairs of spinal nerves emerges it will be seen that this has two roots, a dorsal root which contains a swelling called a **ganglion,** and a ventral root. These unite in a short nerve trunk which then splits up into branches, among which should be remembered a short communicating branch. This

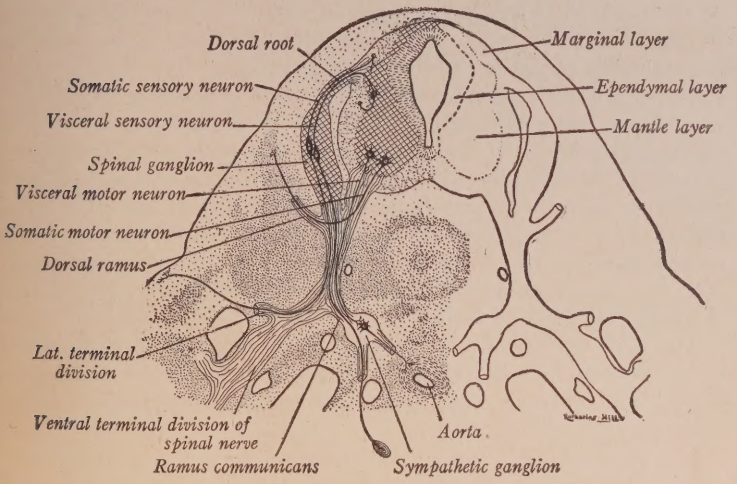

FIG. 19. — Diagram to show the parts of a nerve and the neurones it contains. Based on conditions in a mammal. (See also Fig. 84.) (After Prentiss. From Arey, "Developmental Anatomy," W. B. Saunders and Co.)

runs to a ganglion of the semi-independent autonomic system near the dorsal aorta.

The Neurones. — The neurones which convey impulses to the muscles from the central nervous system are called **motor** neurones. Their bodies lie in the gray layer of the floor and sides of the cord, while their axons pass out through the ventral root of the nerve. Incoming impulses are initiated in the sense organs (see below) and are conveyed from these to the central nervous system by **sensory** neurones, whose bodies lie in the ganglion and whose axons make up the dorsal nerve root.

The Synapse. — The simplest route of a nervous impulse, then, is along a sensory neurone and a motor neurone of the same nerve, as in the case of the knee-jerk. This response, evoked by tapping the tendon below the knee-cap, is due to a two-neurone arc. The neurones concerned do not fuse, as they are separated by a membrane, but come into a state of functional continuity known as the **synapse.**

Intermediate Neurones. — Each neurone may have synaptic relations with several others, as is the case when an impulse conveyed through a sensory neurone located in one nerve is to be transmitted to motor neurones in other nerves. This calls into play a third type known as the **intermediate** neurone. These neurones are contained wholly in the brain and spinal cord.

The Brain. — The brain is divided into five regions, which from the rear are: (1) the **myelencephalon** or **medulla,** connecting with the spinal cord; (2) the **metencephalon,** with an enlargement on the dorsal side called the **cerebellum**; (3) the **mesencephalon,** with two dorsal swellings called the **optic** lobes; (4) the **diencephalon,** with the pituitary gland attached to its floor and the pineal gland arising from its roof; and (5) the **telencephalon,** with the **cerebrum** on the dorsal surface at the posterior end and the **olfactory** lobes in front.

The gray matter of the brain is not continuous as in the cord, but is broken up into groups of intermediate neurones called the higher centers, and a few groups of motor neurones connected with the cranial nerves.

Functions of the Brain. — Attempts have been made, but without great success, to locate the functions of the higher centers of the frog brain by removing portions of the brain and studying the subsequent behavior of the animal. Most of the centers absolutely essential to the continued life of the frog are contained in the medulla, for if all the brain anterior to this be removed, the frog is still able to breathe, snap at food and swallow it, swim, leap, and right itself if turned upon the back. The cerebellum, which in man contains important centers concerned with muscular coördination in relation to equilibrium and the degree of muscle tension (tonus), seems to be of little importance to the frog. The optic lobes, which receive the impulses from the optic nerves, also seem to exercise an inhibiting (restraining) effect upon the spinal responses. These lobes are two in number, as compared with four in man. The diencephalon is principally concerned with the relaying of impulses from one center to

another, and in man the centers for pain are here located. The olfactory lobes of the telencephalon receive the neurones from the nostrils, while the roof (**cortex**) of the cerebrum is but little developed. The human cerebrum is greatly developed and makes up the greater part of the brain. Its gray matter forms a continuous layer known as the cortex, in which areas concerned with particular functions have been mapped out. Some of these are motor and sensory centers, but the greater number are association centers made up of adjustor neurones which form synapses with sensory, motor, and other adjustor neurones to establish innumerable and often extremely complicated routes for the nervous impulses. Over ten million neurones are found in the human cortex, and the synaptic connections possible exceed the limits of imagination.

The Cranial Nerves. — The cranial nerves of the frog are ten in number, as compared to twelve in man. The point at which each originates from the brain, its distribution and principal functions, are indicated in Table II.

TABLE II

Cranial Nerves of the Frog

No.	Name of nerve	Origin in brain	Distribution	Neurones
A.	Terminal[1]	Olfactory lobes	Nose	(?) Sensory
I.	Olfactory	Olfactory lobes	Nose	Sensory
II.	Optic	Diencephalon	Eye	Sensory
III.	Oculomotor	Mesencephalon	Eyeball muscles	Motor
IV.	Trochlear	Optic lobes	Eyeball muscles	Motor
V.	Trigeminal	Myelencephalon	Jaws and face	Mixed
VI.	Abducens	Myelencephalon	Eyeball muscles	Motor
VII.	Facial	Myelencephalon	Jaws and face	Mixed
VIII.	Acoustic	Myelencephalon	Ear	Sensory
IX.	Glossopharyngeal	Myelencephalon	Tongue and pharynx	Mixed
X.	Vagus	Myelencephalon	Throat, lungs, heart, stomach, etc.	Mixed

[1] Not shown in Fig. 18.

Autonomic System. — In addition to the ganglia of the spinal and cranial nerves, other ganglia are found. These ganglia of the autonomic nervous system (Fig. 18) are made up of motor neurones which supply the glands and the visceral musculature. In the frog there are ten such sympathetic ganglia on each side of the dorsal aorta, connected with each other to form two chains. The individual members of these are associated with the spinal nerves by means of the communicating branches referred

to above. They are also connected with smaller ganglia and nerve-nets (**plexus**) found in the walls of the intestine, heart, bladder, etc. This system controls the automatic or involuntary actions of the smooth muscles and the glands.

The Sense Organs. — The nervous impulses transmitted over the intricate network of neurones which we call the nervous system originate from specialized groups of cells or parts of cells known as **receptors** because they receive stimuli from changes in the environment, external or internal, to which they are particularly sensitive. They are highly specialized in respect to the form of energy by which they are stimulated.

Touch. — Thus there are **mechano-receptors** which react only to mechanical stimuli, examples of which are the **tactile** corpuscles of the skin, which are stimulated by being touched. In this group fall the **proprioceptors** of the muscles, joints, and tendons, which indicate the tonus, position, and movements of these organs. Here too belong the equilibrium receptors found in the **semicircular canals** of the ear.

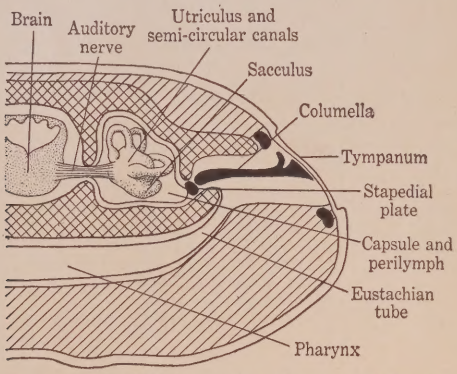

FIG. 20. — *Rana pipiens*, diagram to show the parts of the ear. Schematic cross-section through head.

Sound. — These canals form a part of the ear (Fig. 20), which in the frog has also the function of recording stimuli from sound waves. It is sensitive to wave frequencies of from fifty to ten thousand vibrations per second, while the human ear may be stimulated by frequencies of between sixteen and forty thousand. The frog lacks the outer ear of man, the ear drum or **tympanum** being flush with the surface of the head. Inside

the ear drum is the cavity of the middle ear which opens into the pharynx by means of the **auditory** (Eustachian) tube. Attached to the ear drum is a rod, the **columella,** which extends across the cavity of the middle ear to join a cartilage (**stapedial** plate). This cartilage fits into an oval window in the capsule surrounding the inner ear. The function of this mechanism appears to be that of transmitting energy from the ear drum to the inner ear diminished in amplitude but increased in intensity. The inner ear is a complicated membranous sac lying within the auditory capsule. The sac is filled with a fluid, the **endolymph,** while the capsule contains another liquid, the **perilymph.** Movements of the tympanum are communicated to the columella, thence to the stapedial plate, from that to the perilymph, then to the membranes of the auditory sac, so to the endolymph and thus to sensory cells connected with the acoustic or auditory nerve (VIII). The sensory hair cells are stimulated by sounds of different frequencies so that differences in pitch and quality are distinguishable.

Heat. — Thermo-receptors, sensitive to temperature changes, have not yet been demonstrated microscopically in the frog's skin, but the animal reacts to changes in temperature as if these are present as is the case in man.

Chemicals. — Chemo-receptors are stimulated by chemicals in a fine state of division so that they are capable of going into solution on the surface of the receptor. The olfactory receptors are located in the mucous membrane of the nose and are peculiar in that they are themselves sensory neurones proceeding directly to the olfactory lobes of the brain as the olfactory nerve (I). The taste buds (Fig. 78) of the tongue and inner surface of the mouth are groups of cells with receptor cells each equipped with a sensory hair. Only four tastes exist, sweet, sour, salt, and bitter. Most of the so-called flavors of the human dietary are due to combinations of taste and odor.

Sight. — Photo-receptors capable of stimulation by light are located in the eye (Fig. 21). The eyeball is nearly spherical, covered with tough connective tissue, the **sclera,** which is transparent on the side towards the exterior, known as the **cornea,** and attached to the socket by six eyeball muscles by which it may be twisted in all directions. Light waves pass through the cornea, and into the **aqueous humor,** a fluid filling the eye in front of the **lens.** This is a biconvex transparent body whose position and shape may be altered by the action of attached

muscles. A diaphragm, the **iris,** between the cornea and the lens, regulates the amount of light entering the lens by means of muscles which increase or diminish the diameter of its opening, the **pupil.** The lens focuses the light waves which then penetrate a transparent jelly, the **vitreous humor,** before impinging on the **retina.** This consists of two layers, the outermost of which contains the pigment, which, reflected back through the pupil, gives this structure its individual color. When the pigment is lacking, as in albinos, one sees through the two layers of the retina the capillaries of the **chorioid** layer. The inner layer of the retina contains the actual photo-receptors, modified sensory

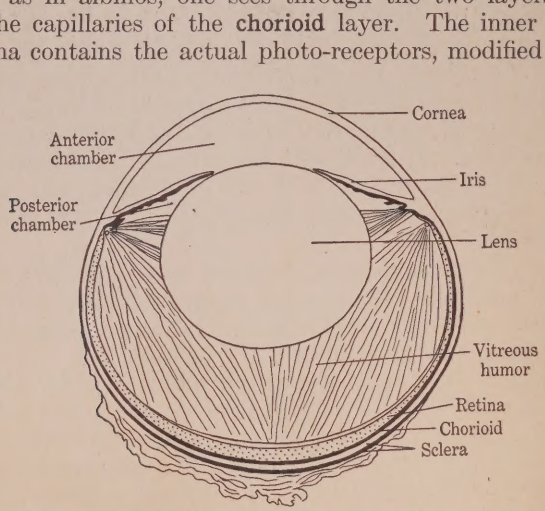

Fig. 21. — Section through eyeball of frog. Modified from Gaupp.

neurones in the form of rods and inverted cones, in which one or more substances, **visual purple** for example, suffer chemical changes and thereby excite the adjustor neurones. Their axones run towards the center of the eyeball and then spread out over the sensory layer of the retina converging towards the blind spot where they leave the eyeball and make up the optic nerve. This makes what is called an inverted eye for the light waves pass through the layer of nerve fibers before arriving at the layer of receptors.

Coördination. — The ear, nose, and eye are the most highly specialized structures built about groups of receptors, and are called the sense-organs. There is some reason to believe that the great development of the cerebrum is connected with the coördi-

nation of impulses originating from the nose, of the optic lobes with the coördination of impulses from the eyes, and of the cerebellum with those from the ear. These three organs are the only ones whose sensory cells are what we may call distance-receptors, and these stimuli of smell, sight, and sound, respectively, must often arrive simultaneously, with consequent problems of coördination.

The Sensory-Neuro-Motor Complex. — Receptors, neurones, and effectors (muscles and glands) make up a **sensory-neuro-motor complex** characterized by its great excitability or irritability. Further consideration of irritability as a cell phenomenon and of the behavior of the organism will be found in Chapter V.

REPRODUCTION

Through the late spring, summer and early fall, the frog leads a solitary and active life in the water, or on the land, engaged in obtaining the food necessary to its continued existence and in avoiding the attacks of its enemies. In the later days of autumn

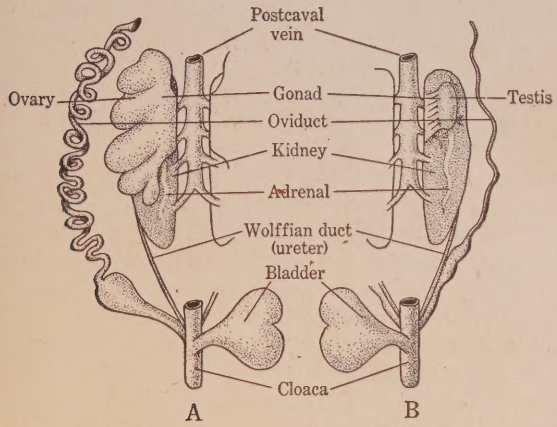

FIG. 22. — *Rana pipiens*, urogenital organs. A, of female; B, of male. Labels in middle column indicate homologies. (After Curtis and Guthrie.)

as the cold weather approaches the frog returns to the water and burrows in the mud to await the return of spring. During this period of hibernation, its vital activities are greatly diminished. No movement is manifest except the slow beating of the heart. No food is taken and the muscular activities of the digestive tube are suspended. The lungs are not in use as the frog obtains its

necessary oxygen through the skin. The energy required for these processes is obtained by the slow consumption of the surplus food stored during the summer in the liver and muscles. But during the winter sleep the frog is engaged in preparing for the spring mating season.

Female Genital Organs. — The female genital organs (Fig. 22 *A*) are the **ovaries** in which the eggs develop, and the **oviducts** by which they are discharged. The ovary is a hollow sac, suspended from the dorsal surface of the body cavity, in the wall of which are found the developing eggs or female germ cells (Fig. 23). During the period of hibernation these are minute rounded cells known as **oögonia.** They multiply by cell division, and those destined to mature in the spring enlarge, principally through the deposition of yolk. This is concentrated in one hemisphere, while the other receives a surface layer of black pigment. During this process the ovaries increase in size and distend the body of the female, because of the great number of enlarged but still immature eggs which are now called **oöcytes.**

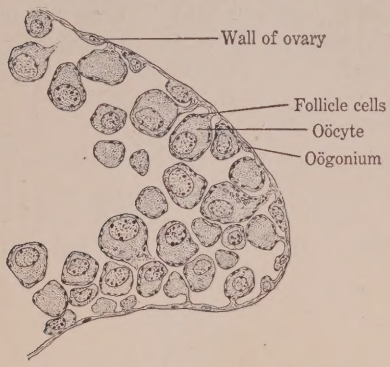

FIG. 23. — *Rana pipiens,* section through part of ovary. ×95.

Male Genital Organs. — The male genital organs (Fig. 22 *B*) are the **testes** in which the sperm develop. They are compact ovoid organs attached to the dorsal wall of the body cavity and are composed of tubules in the walls of which the developing sperm or male germ cells are found. The first stage in the development of the sperm (Fig. 24) is a small rounded cell like the oögonium, which is called in this case the **spermatogonium.** These are engaged in multiplication throughout the year. Some, however, cease division temporarily and enlarge to become **spermatocytes** comparable to the oöcytes of the female. On attaining its full size, each spermatocyte undergoes two divisions in rapid succession by means of which four cells called **spermatids** are formed. These undergo a remarkable transformation in which most of the cell body is sloughed off. The remainder becomes the **spermatozoön,** having the general appearance of a tadpole with a

head and a tail, the lashing motion of which propels the sperm through the water. The tubules in which the sperm develop are connected with the tubules of the kidney, so that the sperm pass through this organ and into its duct, the ureter, which, therefore, also functions as a sperm-duct, whereas the oviduct is vestigial. Just before reaching the cloaca the duct is slightly dilated to afford temporary storage for the sperm before their discharge from the body.

Hermaphroditism. — The early history of the ovary and testis are quite similar, and the testis not infrequently contains eggs, so that it is difficult to distinguish a young male from a female, especially as the male has a diminutive replica of the female duct,

FIG. 24. — *Rana pipiens*, section through part of testis. ×200.

or oviduct. Such males are called juvenile hermaphrodites. True hermaphroditism in the sense that mature eggs and sperm are both produced is, however, quite rare.

Spawning. — When the ice melts from the ponds, the frogs emerge from their burrows and congregate in their favored breeding localities. Now indeed they are far from silent. It has been claimed that the females are guided to the males, which emerge from hibernation first, by the croaking chorus. During this period the arm of the male is more muscular and the thumb enlarged and swollen at the base, while the body of the female is distended by the thousands of eggs in the ovaries.

During the spawning period males and females unite in an embrace called the **amplexus,** in which the male takes his position on the back of the female clasping her body with the forearms. This embrace may last for days. At the onset the eggs are

extruded from the ovary and pass into the oviduct. These convoluted tubes open into the body cavity near the ovaries and the eggs enter the tube through this opening. The oöcyte undergoes an unequal division which results in the pinching off of a small cell called the first **polocyte** (Fig. 25). As the eggs pass down the oviduct they receive a thin coating of jelly secreted by the walls of the oviduct. The posterior end of this tube is enlarged to form a thin-walled and distensible sac, the **uterus,** in which the eggs collect. Finally the eggs are extruded from the

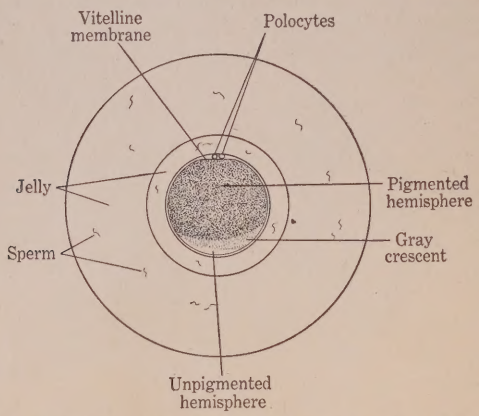

FIG. 25. — *Rana pipiens.* Fertilized egg and membranes. Slightly schematic. ×10.

cloaca accompanied by a small amount of jelly, while the male discharges over them a stream of **milt** containing millions of spermatozoa.

Fertilization. — Each egg is fertilized by the entrance of a single spermatozoön. After this the egg undergoes a second division by which a second minute polocyte is produced. These two divisions of the oöcyte are comparable to the two divisions undergone by the spermatocyte. Their theoretical importance will be discussed in Chapter VI. The thin layer of jelly surrounding each egg swells by the absorption of water until it is two or three times the diameter of the egg in thickness. As the female generally clasps a waterplant or stick while spawning, the spawn adhere to this and form a gelatinous mass four or five inches across, containing from three to five thousand eggs, each of which is a potential frog.

Artificial Parthenogenesis. — In fertilization, one spermatozoön enters each egg, which thereupon extrudes a liquid and so elevates the egg (**vitelline**) membrane that the egg may rotate inside, coming to rest with the black hemisphere uppermost. Unless fertilized the egg never develops further. In the laboratory, however, a treatment involving puncturing the egg with fine glass needles has been successful in producing the later stages of development. This is called artificial **parthenogenesis.** Natural parthenogenesis (Chapter VI) though common in some animals is unknown in the frog.

The Gray Crescent. — The external evidence of the successful fertilization of the egg is the appearance of a gray crescent (Fig. 25) between the black and white hemispheres on the side of the egg opposite to that which the spermatozoön entered. This is apparently caused by the slipping of the surface layer of the egg which contains the black pigment towards the point where the entrance of the spermatozoön took place.

Cleavage. — The fertilized egg now enters upon a period of cell division called **cleavage** (Fig. 26). From the center of the

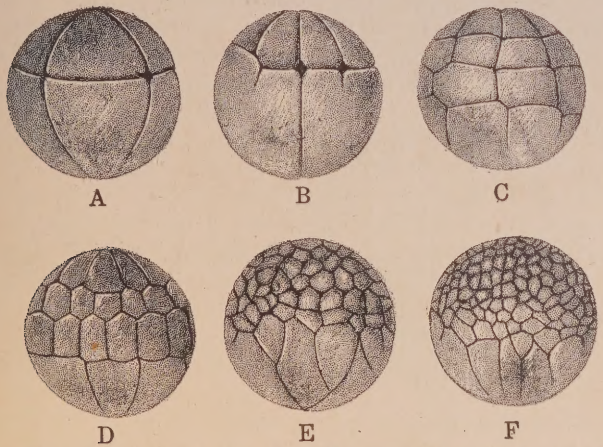

FIG. 26. — Cleavage in the frog's egg. A, third cleavage; B, fourth cleavage (12 cells); C, fifth cleavage; D, sixth cleavage; E, F, later stages. (From Shumway, "Vertebrate Embryology," after Morgan.)

black hemisphere, at the point where the polar bodies were formed, a furrow grows down, usually bisecting the gray crescent, until the ends meet in the center of the white hemisphere. This

furrow deepens until the egg is completely divided, at the end of an hour and a half, into two daughter cells called **blastomeres.** New cleavage planes, each dividing the blastomeres already formed into equal halves and usually at right angles to each other, produce four-cell, eight-cell, sixteen-cell stages, and so on, each new cleavage taking about an hour at first. The cleavage planes parallel to the equator of the egg usually divide the cells into unequal parts, the lower yolk-laden blastomeres being the larger. Cleavage continues to subdivide the egg into smaller and smaller cells until, after about twenty-four hours, a slight groove in the region of the gray crescent and parallel to the equator of the egg marks the beginning of germ layer formation.

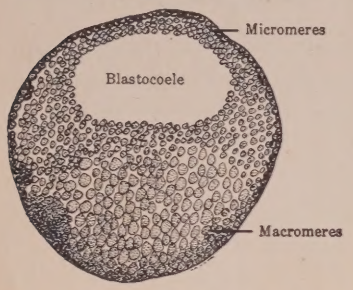

FIG. 27. — Section of blastula of frog. (From Shumway, after Brachet.)

The Blastula. — The egg just prior to the appearance of this groove is said to be in the **blastula** stage (Fig. 27). Its diameter is but little larger, one-fifth, to be exact, than before, but it is composed of many cells. Those in the black hemisphere are now too minute to distinguish with the naked eye, while those in the white hemisphere are still large enough for visibility on account of the retarded division-rate in the lower yolk-laden half of the egg. If the egg be split in two, a cavity, the **blastocoele,** is apparent in the upper hemisphere. This first appeared in the eight-cell stage due to the rounding up of the blastomeres after each division. Four or more layers of cells surround this cavity.

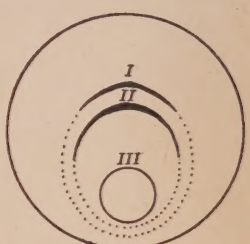

FIG. 28. — Diagram showing three stages in the formation of the blastopore in the frog's egg. (From Shumway, after Morgan.)

Germ Layer Formation. — The cells in the vicinity of the gray crescent divide more rapidly than elsewhere, thus bringing about the appearance of the groove mentioned above (Fig. 28). The cells along this groove change their shape and withdraw beneath the surface as the groove itself moves down the side of the egg, gradually lengthening and assuming first a semicircular and

finally a circular appearance. The yolk-laden cells are now completely covered by the proliferating black cells except inside this circle, now known as the **blastopore,** where they protrude slightly to form a yolk-plug. The inturned cells referred to above form the roof of a new cavity called the **gastrocoele** (Fig. 29), the walls and sides of which are lined by small cells derived from the large yolk blastomeres. Later by proliferation and migration these cells form a roof beneath the layer made up of the cells derived from the dorsal lip of the blastopore. There are now three layers of cells in the embryo. The surface cells are called the **ectoderm;** those which line the gastrocoele make up the **endoderm;** while the middle layer, derived from the dorsal lip of the blastopore, forms the **mesoderm** ("chorda-mesoderm"). The position of the blastopore marks the posterior end of the embryo, while a flattening on the dorsal surface is the neural plate. The embryo is now called a **gastrula.**

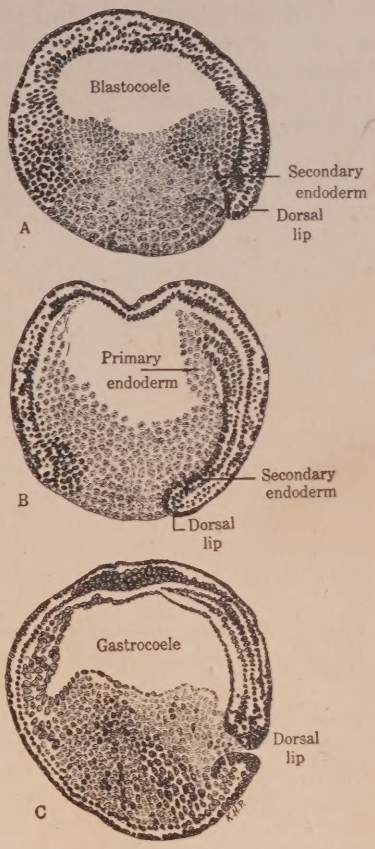

FIG. 29. — Sagittal sections showing three stages in the gastrulation of the frog's egg. (From Shumway, after Brachet.)

The Germ Layers. — From the germ layers whose origin has just been described the organs of the body are gradually differentiated. The ectoderm gives rise to the epidermis of the skin, the nervous system, and the receptors of the sense organs. The digestive tube and all its derivatives such as the liver, pancreas, urinary bladder, and lungs are lined with endoderm. The remainder of the body is formed from mesoderm,

which is the original source of the skeleton and muscles, blood vessels, excretory and genital organs. Even during the period of gastrula formation, the **primordia** (beginnings) of some of these organ systems are localized. Thus the thickening and flattening of the dorsal ectoderm (**neural** plate) is the first indication of the sensory-nervous complex, the gastrocoele is the primordium of the digestive tube, while along the median line of the inturned mesoderm, an axial rod, the **notochord,** forms the primordial skeleton.

The Early Embryo. — The embryo now enters upon a period of growth and further differentiation, still within the egg jelly, until at the end of two days, more or less, according to the tem-

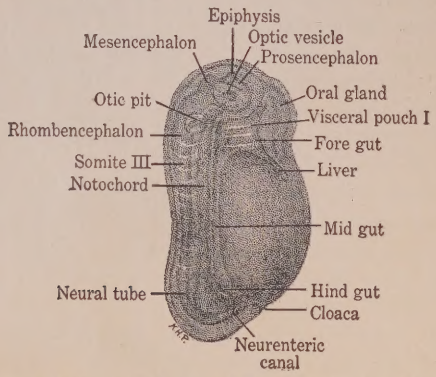

Fig. 30. — *Rana pipiens*, lateral view of 3 mm. embryo. Cleared specimen. ×15. (From Shumway.)

perature, it has attained a length of three millimeters (Fig. 30). The head region through its more rapid growth has become distinguishable from the trunk, in which a well-marked bulge on the ventral side indicates the presence of the yolk. A tail bud is present.

The neural plate has become transformed into a neural tube through the growth of folds rising along its edge and finally fusing along the mid line. The narrow strip of ectoderm connecting the tube with the overlying epidermal ectoderm forms the neural crest from which the ganglia will develop. The epidermis becomes ciliated, that is to say, the cells of the ectoderm develop movable hairs, by means of which the embryo rotates within the egg jelly.

The chorda-mesoderm formed at the dorsal lip of the blastopore gives rise to the median axial notochord, and to sheets of mesoderm on each side. The portion of each sheet adjacent to the notochord is divided by transverse constrictions into a series of small blocks called **somites.** The portion of the sheet on each side of the gut splits tangentially so that an outer layer of **somatic** mesoderm is applied to the ectoderm and an inner **splanchnic** layer is applied to the endoderm. The cavity between these is the body cavity or coelom. These layers are connected with the somites by an intermediate mass of mesoderm which is cut into transverse segments known as **nephrotomes.** In the head region these are enlarged to form the primordium of the head-kidney or **pronephros.**

The gut is divided into a large cavity in the head known as the **foregut,** from which three narrow visceral pouches extend to the exterior. The **midgut** is a compressed canal overlying the mass of yolk-laden cells which represents a yolk sac. From the foregut a tongue-like cavity extends back into this mass of yolk cells. It is the primordium of the liver. The midgut continues into the **hindgut,** connected with the neural tube by a **neurenteric** canal and opening to the exterior by means of the cloaca, which was formed by the ingrowth of an ectodermal pit. The primordium of the mouth at the anterior end is a groove, on either side of which a heavily pigmented area is the primordium of the **oral** gland or sucker.

Attention may be called to the primordia of several other structures which are better developed at the next stage. On the dorso-lateral margins of the mouth, thickened areas (**placodes**) represent the nostrils. Lateral bulges on either side of the head are caused by the optic **vesicles** (hollow sacs) growing out from the brain — the primordia of the eyes. Posterior and dorsal to these are very slight bulges due to the auditory vesicles, which arose as placodes, invaginated (pushed inward) to form pits, and finally were closed over and pinched off to become the primordia of the inner ears. Ventral to these are the **gill** plates, each of which has five dorso-ventral furrows known as the visceral grooves. In spite of the number of structures thus far localized there is very little difference between the tissues of these organ primordia.

The Early Larva. — At the time of hatching from the egg jelly, the muscles have developed so that the embryo is able to execute violent twitches, which together with the less viscous

state of the jelly enable it to free itself. It now attaches itself to the mass of jelly by means of its sucker until the mouth opens and it is able to take in food. The length at which the embryo hatches varies between three and six millimeters, according to whether the temperature has been warmer or colder, and its age varies between one and two weeks. The six-millimeter stage (Fig. 31) is described as more representative of normal conditions.

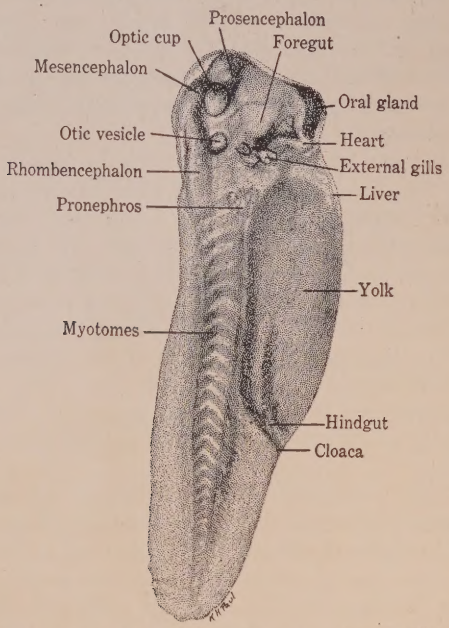

FIG. 31. — *Rana pipiens*, lateral view of 6 mm. embryo. Cleared specimen. ×15. (From Shumway.)

The mouth has not yet opened into the foregut so that the early **larva** (as the just-hatched stage is called) is still dependent upon the contained yolk for food. The deepening of the pit, however, is accompanied by the appearance of ridges which are the primordia of the jaws. The olfactory organs are now pits connected with the mouth pit by grooves. The primordia of the cement glands have fused to form a V-shaped organ. The visceral pouches, now five in number, have not yet joined the visceral grooves, while on the third and fourth of the visceral arches,

between the grooves, branching projections represent the external gills. Behind these a bulge, the pronephric elevation, continues back as the pronephric ridge overlying the duct of this early kidney. Intersomitic grooves are apparent, and the tail is now bilaterally compressed.

The epidermis is still ciliated, and the early larva creeps along propelled by the oar-like motion of these tiny hairs. A more typical mode of locomotion is seen in the wriggling motion of trunk and tail which may be stimulated by a slight touch, showing that the development of the sensory-neuro-muscular complex has begun. From the ganglia which have arisen from the neural crest, masses of ganglion cells have separated and are advancing towards the mid line of the body to form the sympathetic ganglia. The optic vesicles are invaginated optic cups, while in the ectoderm external to each a lens placode has invaginated and separated from the overlying ectoderm. A **lateral line** placode extends the length of the tail and will give rise to the lateral line organ, a group of receptors sensitive, apparently, to water currents.

From the somites, masses of striate muscle cells are differentiated, particularly in the tail region. The nephrotomes in the head have acquired cavities which open into the coelom by means of ciliated apertures. These cavities elongate to become the pronephric tubules, the first excretory organs, and each grows backward at its dorsal extremity to form the pronephric tube which empties into the cloaca. A mass of capillaries from the dorsal aorta bring the blood to the pronephros. The heart at this time is a twisted tube, extending from the point at which two vitelline veins conveying blood from the midgut unite with each other, to the point where it divides into the aortic arches. These pass through the visceral arches to fuse on the dorsal side of the foregut and give rise to the dorsal aorta which supplies the various organs.

From the floor of the pharynx a groove marks the beginning of the thyreoid gland. The neurenteric canal has disappeared.

The Young Tadpole. — During the next two weeks the larva assumes the tadpole appearance. In a young tadpole of nine-millimeter length (Fig. 32), head and trunk are fused in a common ovoid mass, sharply distinguished from the long bilaterally compressed tail. The mouth is open and circular and armed with horny raspers, while the oral gland is vestigial. The large eyes protrude from either side on the dorsal surface. Anterior to these the nostrils are now tubes opening into the mouth. The

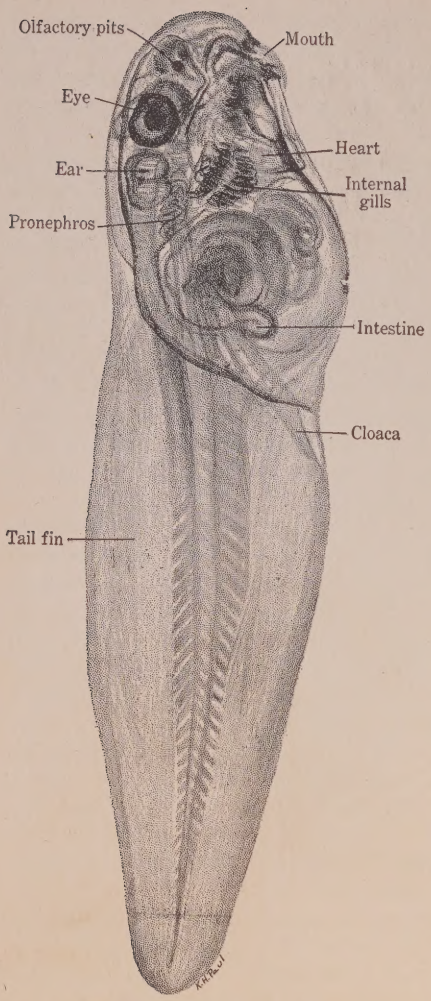

FIG. 32. — *Rana pipiens*, lateral view of 9 mm. larva. Cleared specimen. ×15. (From Shumway.)

external gills have degenerated after having been covered by flap-like overgrowths, **opercula,** arising from the second visceral arch. Their functions have been taken over by internal gills which developed on the third, fourth, and fifth visceral arches when the pouches and grooves finally united to form visceral clefts. The water taken into the mouth pours out through these visceral clefts, while capillaries in the gills make a respiratory exchange before the water escapes through the opercular pore on the left side. The tail, now two-thirds of the entire body length, has a well-marked fin.

The epidermis has lost all traces of cilia, the brain has a well-developed cerebrum, optic lobes, and cerebellum. All cranial and spinal nerves are established as well as the autonomic system. The pineal gland and pituitary glands are formed. The eye is well developed and functional; the ear still lacks its semicircular canal.

The skeleton has not advanced far in development. Masses of cells from the somites will shortly invest the notochord to form the vertebrae, while about the brain and sense organs, a cartilaginous skull will soon

develop. The muscles are well developed. The pronephros is still the functional kidney. The coelom is divided by a transverse partition into an anterior **pericardial** cavity containing the heart and a posterior **visceral** cavity in which the other viscera are located. The heart is divided into a muscular ventricle and a thin-walled auricle. Four aortic arches are present. The vitelline veins are broken up into a portal vein which carries blood to the liver and hepatic veins which carry it thence to the heart. From the head the blood is returned by paired anterior **cardinal** veins, from the tail by posterior cardinals which unite with the others to form the common cardinal veins running to the heart. This type of circulatory system is quite characteristic of the fish, and suits the aquatic method of life of the tadpole.

The digestive cavity now forms a long tube from mouth to vent. The tongue is present, and the pharynx opens into the opercular chamber by four visceral (gill) clefts on each side. Thymus and parathyreoid glands have arisen from the visceral pouches, and the thyreoid has separated from the pharynx. Larynx and lungs have arisen from a median ventral out-pushing (evagination) of the pharynx. The stomach is hardly distinguishable from the oesophagus and intestine. The liver has increased greatly in size and its duct receives the secretions of the pancreas, which arose as a separate structure. The intestine, greatly elongated, is coiled in a double spiral which terminates in a rectum opening into the cloaca. No urinary bladder is present.

Metamorphosis. — The larval period is terminated by a sudden metamorphosis (Fig. 33) of the tadpole into a frog, which occurs in late summer, three or four months after fertilization. The legs develop at the base of the tail, followed by the appearance of the arms. The left arm appears first, through the opercular aperture. The tail is gradually resorbed. The skin is cast off and with it the horny raspers, while the circular mouth elongates from side to side. The eyes enlarge and protrude while the ear drums make their appearance.

Gills and gill slits disappear, and the aortic arches are once more continuous from ventral to dorsal aorta. The lungs complete their development and acquire the pulmonary arteries and veins. The stomach dilates, and the intestine shortens until it is less than one-third of its original length. The pronephros degenerates and its functions are assumed by a larger and more complicated organ, the **mesonephros,** or adult kidney. Ovary and testis increase in size.

The frog grows rapidly during the late summer and fall and during the following year. In the spring of the second year it becomes sexually mature, and thereafter growth practically ceases.

The Life Cycle. — The life cycle of the frog occupies a period of two years, from the fertilization of the egg until the new individual is in its turn able to produce mature germ cells. During this period we distinguish the following periods: (1) the fertilization of the egg; (2) the period of cleavage, terminating

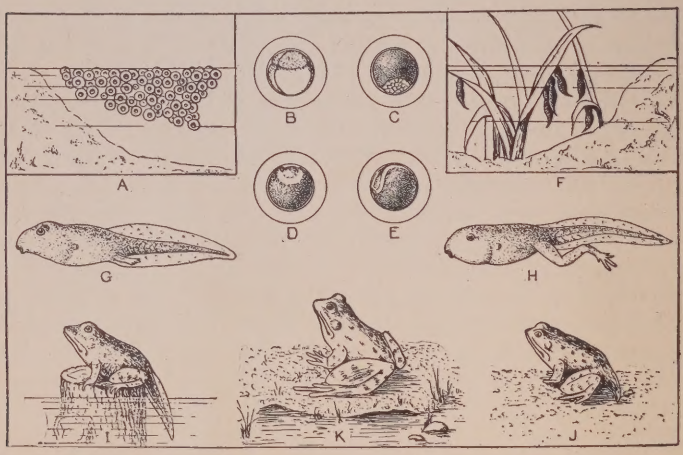

FIG. 33. — *Rana pipiens*, life history. A, spawn; B, cleavage; C, D, germ layer formation; E, neural fold stage; F, after hatching; G, larva commencing metamorphosis; H, I, J, later stages in metamorphosis; K, young frog. (From Curtis and Guthrie.)

in the blastula; (3) the period of germ layer formation, terminating in the gastrula; (4) the period of early organogeny, terminating in hatching; (5) the larval period, terminating in metamorphosis; (6) the period of adolescence during which the individual slowly attains to (7) sexual maturity. This may be followed by a period of (8) senescence or old age terminated by death.

Natural death is probably extremely rare among frogs. Their amphibious mode of life makes them the natural prey of fish, larger frogs, turtles and snakes, water birds and carnivorous water mammals. But even if protected from all these as well as

from disease, starvation, and too violent extremes of temperature, the life of the frog cannot continue indefinitely. Eventually the activities of the body gradually slacken until they are terminated by death. The natural span of the leopard frog's life is unknown, but bull frogs have attained the age of nine years.

CHAPTER III

A FLOWERING PLANT

No single flowering plant has obtained such a dominating position in the botanical laboratory as has the frog in the zoölogical course. Great attention, however, has been paid to the wheat plant because of its world-wide distribution and economic value. As a highly organized plant species it will serve for comparison with the highly organized animal, the frog, which has just been examined in detail. Sown in the fall or the spring and harvested in the summer, it can be examined in the field during the college year. The seeds are easily germinated in the laboratory and the size of the plant is not too large for convenient study. The flower, to be sure, differs widely from the pattern flower, but it can easily be described in terms of the latter. Its annual life cycle is no disadvantage except that the formation of wood plays no part in its life.

THE WHEAT PLANT

The common wheat, *Triticum aestivum* (Fig. 34), is built on a very different plan from that of the vertebrate animal. The frog is bilaterally symmetrical, with its principal axis parallel to the earth's surface along which it moves. The wheat plant approaches more nearly to a radial symmetry since any one of a number of planes will bisect the body into halves which are approximately mirror images of each other. Its principal axis is at right angles to the surface of the earth to which it is securely anchored.

The vertebrate grows in length along its principal axis until it attains sexual maturity, when growth diminishes if it does not cease entirely. The annual plant grows in length along its principal axis until it attains sexual maturity, which is followed by death. The metabolic activities of the frog are expressed chiefly in terms of muscular activity. The metabolic activities of the wheat are expressed for the most part in growth. The reproduction of the frog is an annual incident in the life cycle; in the wheat plant it is the culmination of that cycle.

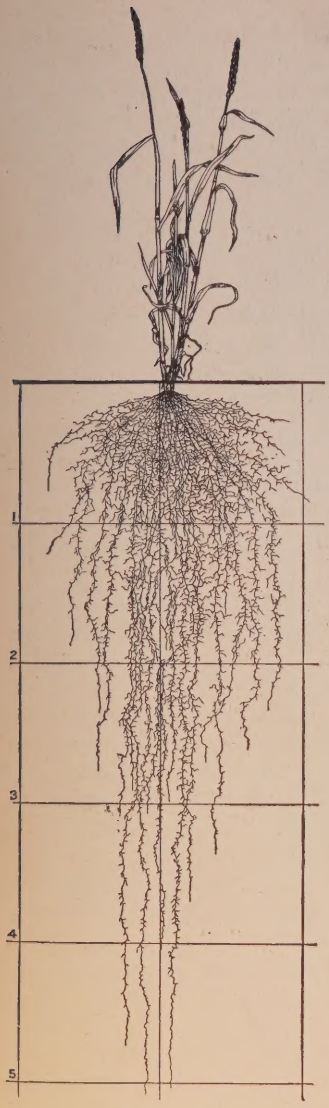

FIG. 34. — *Triticum aestivum*, the wheat plant. The numbers represent the depth in feet of the roots. (From Holman and Robbins.)

We shall give first a short account of the annual life cycle of wheat, then a description of the structure and activities of the wheat plant, and conclude with a detailed account of its development.

The Annual Life Cycle. — The seed of the wheat contains a rudimentary plant, known as the embryo, which may have been dormant in a resting stage for a very long period of time. The germination of the seed implies a resumption of growth. Growth proceeds in both directions, downward as the root, upward as the shoot. The young plant which presently makes its way above ground is known as a seedling (Fig. 35).

FIG. 35. — Wheat seedling, showing particles of soil attached to the root hairs. The tips of the roots are hairless. See also Fig. 56. (From Holman and Robbins.)

Roots, stem, and leaves are formed as growth continues, and after the plant has gone through a period of vegetative activity flowers are produced. This marks the assumption of sexual maturity, for the flower contains both male and female elements. In the course of development, a part of the female flower becomes the fruit, of which the seeds contain embryos.

METABOLIC ACTIVITIES

The wheat plant consists of root and shoot. The root anchors the plant and is the organ whereby the plant absorbs water and inorganic salts from the ground. The food of the wheat like that of the frog contains carbohydrates, lipins, and proteins, but unlike the frog, the wheat is able to manufacture these organic compounds from simple inorganic salts, water, and carbon dioxide. The carbon dioxide is obtained from the atmosphere. From the soil the wheat obtains water and, in solution, nitrates, phosphates, and sulphates of potassium, calcium, magnesium, and iron.

Absorption and Anchorage (the Root). — The root of the seedling develops five regions: (1) the **root cap,** (2) the **growing point,** (3) the **region of elongation,** (4) the **zone of root hairs,** and (5) the **mature region.** The root cap is a mass of loose cells fitted over the growing end of the root which protects it from abrasion as it is thrust down into the soil. It is constantly being worn away by the soil and as constantly replenished from the cells produced at the growing point. Behind this region of rapid cell division, the daughter cells grow quickly in length and form three primary **meristems** or elementary tissues (compare the germ layers of the frog embryo). The outermost of these is the **protoderm,** the middle layer is called the **ground meristem,** and the innermost tissue is the **procambium.**

The Root Hairs. — In the next region, the zone of root hairs, these meristems have given rise to five permanent tissues. The **epidermis,** a single layer of cells from which the root hairs arise, is the outermost layer and is derived from the protoderm. The root hairs are the structures by which absorption is carried on. They are individual cells of the epidermis which elongate greatly and stretch out into the surrounding soil. They are short lived and survive only a few days or weeks, for as the root grows through the soil, new hairs are formed. The zone of elongation

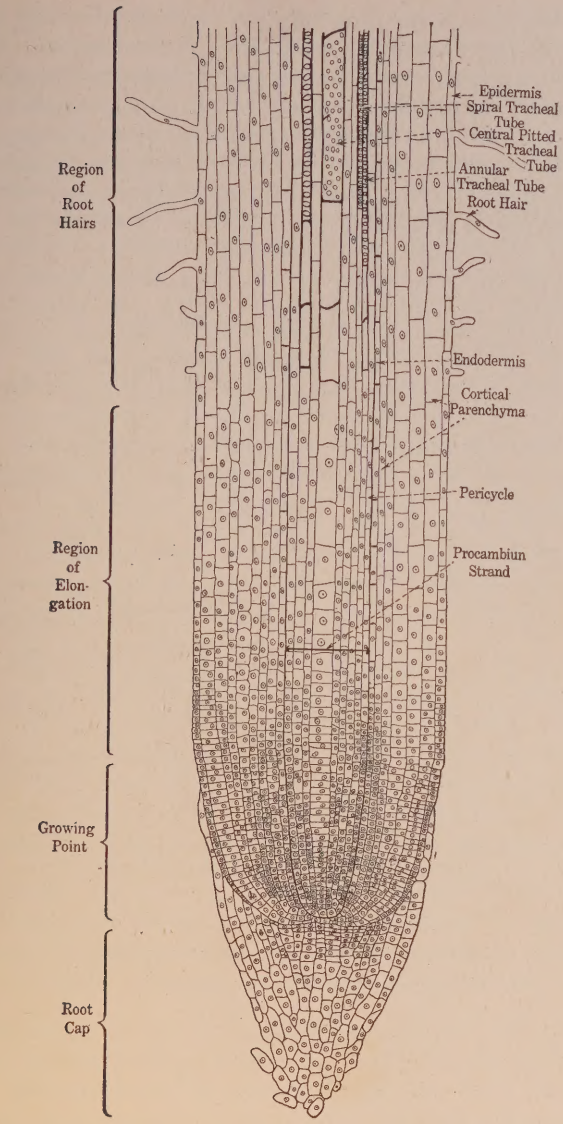

FIG. 36. — *Hordeum sativum* (barley), longitudinal section of root. (From Holman and Robbins.)

becomes the zone of root hairs, and as the older ones die the zone of root hairs becomes a part of the mature region. In this way the root gains access to new stores of water and salts while it leaves behind accumulated wastes which it has excreted. The root hair also acts in a limited way as a respiratory organ, for it obtains the oxygen needed for its own metabolism directly from the soil and gives off a small amount of carbon dioxide. All substances which enter the root hairs do so in solution in water.

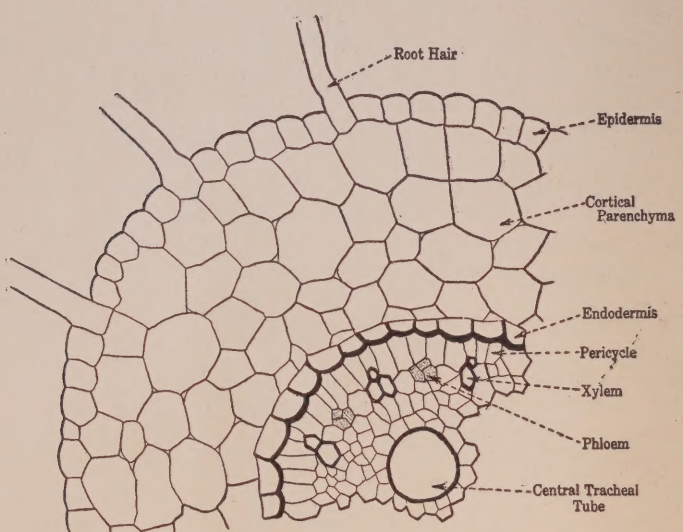

FIG. 37. — *Hordeum sativum* (barley), cross-section of root in root hair zone. (After Percival, from Holman and Robbins.)

The carbon dioxide excreted may remain united with water as carbonic acid which aids in dissolving some of the minerals of the soil.

The Cortex. — The **cortex** is the next layer and is formed from the ground meristem. It is primarily a connective tissue (**parenchyma**) the innermost layer of which is the **endodermis.** This is a thin layer of cells also derived from the ground meristem and surrounds the **pericycle,** another derivative of the ground meristem.

The Vascular Cylinder. — The water and soluble salts absorbed by the root hairs diffuse through the cortex and pericycle to the **vascular cylinder,** derived from the central procambium. The vascular cylinder contains alternate groups of **xylem** and **phloem** strands surrounded by parenchyma. The xylem is made up principally of long **tracheal tubes,** each composed of a linear series of empty elongate cells with thickened side walls, but from which the end walls have been dissolved away. Through these the water and inorganic salts make their way up the root. The phloem contains long **sieve tubes,** vertical rows of cells in which the end walls are pitted like sieves. Through these the sap with the contained manufactured foods passes down from the shoot. The parenchyma internal to the row of xylem and phloem strands is continuous with the pith of the stem which is sometimes hollow.

The Root System. — The root of the seedling with its branches, which originate from the pericycle and grow out through the cortex and epidermis, form a temporary root system. The permanent fibrous system arises in whorls at the joints in the stem, the first appearing about an inch below the surface of the ground. Other whorls appear successively above the first and thus give rise to the fibrous root system which may extend as much as five feet into the ground.

Conduction and Support (the Stem). — Like the root, the shoot grows continuously during the vegetative period. This growth occurs at a terminal growing point, which like that of the root is an actively growing mass of cells. It is surrounded by rudimentary leaves which together with it form the terminal bud. In the **axil,** or point of junction with the stem, of each leaf is the primordium of another or lateral bud, which also has a growing point and rudimentary leaves. As the terminal growing point increases the length of the shoot, we may distinguish the **culm** or stem from the leaves. The regions in which the leaves arise are known as **nodes** (joints), and the regions between these are the **internodes.** The base of each internode remains relatively undifferentiated as a meristem which continues growing long after the upper portion has ceased to do so.

Tillering. — In addition to the principal stem which arises from the seed, branches are produced from the axillary leaf buds of the lowermost node of this stem, thus giving rise to a shoot system with secondary and tertiary stems. This process is known as **tillering** (or stooling) in cereals such as wheat (Fig. 38).

Meristems. — The growing point of the shoot like that of the root soon becomes differentiated into the three primary meristems, protoderm, ground meristem, and procambium, but the last meristem instead of forming a central vascular cylinder gives rise to a circle of procambium strands each of which will become a **vascular bundle.**

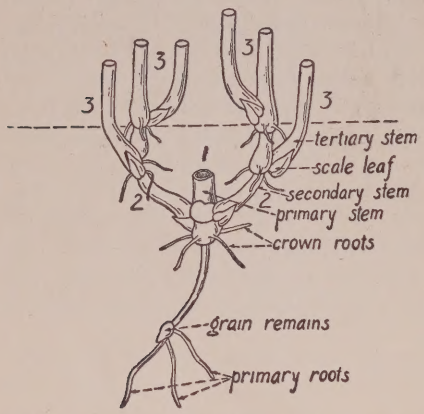

FIG. 38. — Diagram showing tillering. (After Schindler, from Holman and Robbins.)

Tissues of the Stem. — The protoderm gives rise to the epidermis; the ground meristem gives rise to cortex and pericycle of the parenchymatous type, although the outermost layer of cells may contain chlorophyll (see page 62); the procambium strands form xylem and phloem only, without parenchymatous tissue (closed vascular bundles). The internodes are hollow, without a pith.

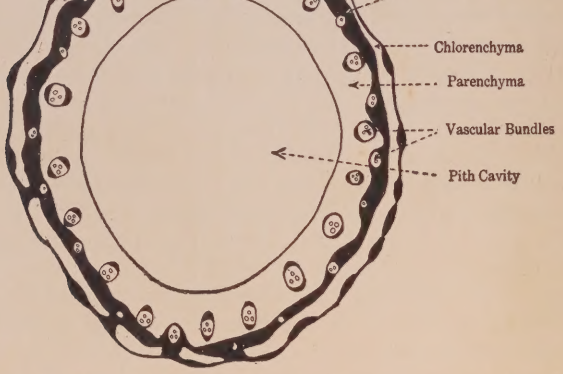

FIG. 39. — *Secale cereale* (rye), cross-section of stem. (After Nathanson, from Holman and Robbins.)

Rise of the Sap. — The functions of the stem are almost entirely those of support and conduction, although some photosynthesis (see page 61) does occur. The rise of the sap through the xylem is due in part to pressure occasioned by the absorption of water by the roots but primarily to the transpiration of water by the leaves (see page 60). Nutritive materials in solution pass down the phloem.

Photosynthesis, Transpiration, and Respiration (the Leaf). — The leaf is essentially an expanded lateral outgrowth of the stem arising at a node and having a bud in its axil. The form of the leaf is compressed to form a larger absorptive surface. The wheat leaf completely incompasses the base of the internode to form a **sheath,** but finally opens up as the **blade.** Where the two join is a scale-like structure known as the **ligule.** It is said that this prevents water draining down the blade into the sheath.

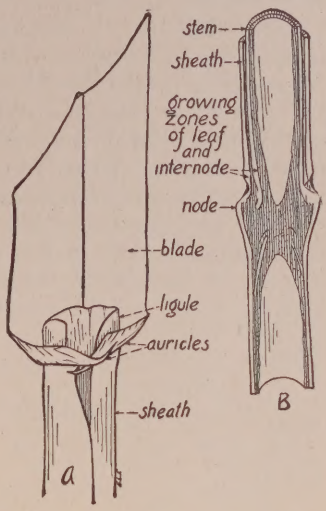

FIG. 40. — *Hordeum sativum* (barley), leaf. A, junction of leaf and stem; B, longitudinal hemi-section of stem. (From Holman and Robbins.)

Tissues of the Leaf. — Three tissues make up the leaf: the epidermis, a layer of covering cells, containing at intervals pairs

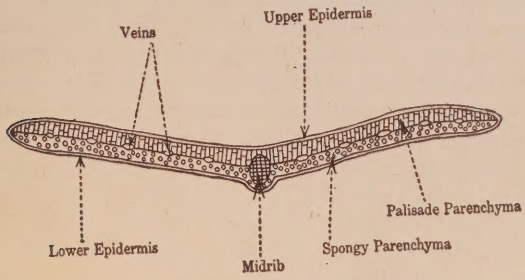

FIG. 41. — Diagram to show structures of a typical leaf in cross section. (From Holman and Robbins.)

of **guard** cells which surround the **stomata,** openings leading into large air chambers in the middle layer, the **mesophyll.**

Through the mesophyll runs the **midrib** with its branching **veins** and **veinlets,** which are vascular bundles, connecting with those of the stem.

Transpiration. — The epidermis controls the rate of transpiration, or loss of water vapor by means of the guard cells (Fig. 42). These open or close the stomata according to the amount of their water pressure (**turgor**). When this is greater than that of the surrounding cells, the cell wall bulges out in such a way as to open the stoma. When it is equal to that of their neighbors their median walls come into contact with each other, thus closing the stoma. Illumination of the leaf by sunlight increases the concentration of sugar in the guard cells by photosynthesis (see below) so that they draw water by osmotic pressure (see page 94) from their neighbors. This increases their own turgor and bulges out the thinner side of the cell wall away from the stoma, thus creating an opening. When the leaf is not illuminated, the excess sugar diffuses out from the guard cells to their neighbors or is converted into starch. The turgor decreases, the walls return to their normal position, and the stoma is closed.

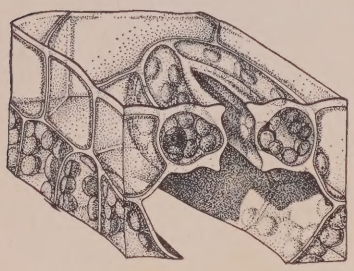

FIG. 42. — Diagram to show a stoma with its guard cells and neighboring epidermal cells. (From Holman and Robbins.)

The evaporation of water vapor from the stomata is as essential to the life of the wheat as is the beating of the heart to the life of the frog. The circulation of the frog is, however, a closed system of conduction, whereas that of the plant is an open system, in which water is constantly absorbed by the roots and transpired by the leaves. There is therefore a greater vigor and volume of flow in the xylem than in the phloem. Factors affecting the rate of transpiration are the humidity of the atmosphere, its temperature and air currents, the intensity of illumination, and the water content of the soil. The greater the humidity, the less the transpiration. This causes the phenomenon known as **guttation,** when drops of water form on the leaf during cool moist nights after hot summer days. Air currents sweep away the mantle of moist air surrounding the leaves and thus increase the rate of transpiration. A rise of temperature increases the rate of transpiration and vice versa. Low tempera-

tures, low water content, or excessive concentration of solutes in the soil reduce the rate of absorption, conduction and, therefore, of transpiration. When the rate of transpiration exceeds that of absorption the leaf wilts.

The Mesophyll. — The mesophyll of the typical foliage leaf is made up of parenchymatous tissue of three kinds. The upper portion of the leaf is made of **palisade** parenchyma, several layers of cells elongated at right angles to the leaf surface. The lower portion is **spongy** parenchyma, containing numerous and large air chambers which communicate with the smaller intercellular spaces of the palisade parenchyma. The latter, however, is more richly provided with **chloroplasts** (see page 85), the centers of photosynthesis. The **border** parenchyma contains no chloroplasts or intercellular spaces and forms a single layer of cells about the veins and veinlets.

In the blade of the wheat leaf the veins visible to the naked eye run parallel to the midrib, which they join at the base. Small veinlets connect the veins. The midrib and larger veins support the blade and serve as vascular bundles which connect with those of the stem. The veins are composed of xylem in the upper portion of the bundle and phloem in the lower part. The veinlets are composed exclusively of xylem made up of **tracheids,** single dead cells, elongate and hollow.

Conduction. — The water absorbed by the root hairs passes through the cortex, endodermis and pericycle and thus into the vascular cylinder of the root. This is in direct continuity with the vascular bundles of the stem, which at the nodes send out branches to the leaves. Each branch continues into the leaf as the midrib which divides into veins and these into veinlets. From the veinlets the water diffuses through the cells of the mesophyll and evaporates from them into the intercellular spaces and escapes as water vapor through the stomata. The pull exerted by transpiration in addition to the push resulting from root pressure lifts the water the height of the stem, which in trees may be very great.

The products of photosynthesis are passed through the border parenchyma cells until they reach a vein with phloem elements, the sieve tubes of which conduct them to the midrib and finally to the phloem of the stem.

Photosynthesis. — In the palisade and spongy parenchyma of the leaf, as well as in the cells of the stem cortex which possess chloroplasts, water is combined with carbon dioxide in the presence

of sunlight to form carbohydrates. This process is known as **photosynthesis** and is the only biological synthesis in which the energy required is not supplied by the simultaneous decomposition of other substances within the organism. The energy of the sun is converted into potential energy stored in the organic compounds produced. Thus water and carbon dioxide contain no potential energy, while the simple carbohydrate glucose produced by photosynthesis contains four **calories**[1] per gram when oxidized.

Carbon Dioxide. — The carbon dioxide which is normally present in the atmosphere, making up about .03 per cent of its volume, diffuses through the stomata into the intercellular spaces and goes into solution in the film of water on the surrounding parenchyma cells, and thence makes its way into the cells. "The maximum amount of photosynthesis under natural conditions is said to involve the absorption of 820 cubic centimeters of carbon dioxide per square meter of leaf surface each hour. That amount of carbon dioxide would be contained in an air column of 1 square meter cross-section and $2\frac{1}{2}$ meters high" (Holman and Robbins).

Energy. — The energy utilized is derived from the radiant energy of the sun, which passes through the transparent epidermis and is absorbed by the green chloroplasts. These self-reproducing organs of the cell have a surface layer of **chlorophyll,** a mixture of two green lipin compounds, and contain also two yellow pigments, **carotin** and **xanthophyll.** The chloroplast is a colorless body at first, turns green as the chlorophyll develops and finally becomes a yellowish brown as the leaf dies in the fall. These pigments absorb a large part of the red-orange region of the spectrum (Fig. 43) and a portion of the blue-violet, the reflected green rays giving the leaf its characteristic color.

We may think of the chlorophyll as an energy transformer which steps up the energy from the red end of the spectrum to an intensity comparable to that of ultra-violet light which can effect the reduction of carbon dioxide and water to sugar without the intervention of chlorophyll. With certain enzymes in the cell it acts as a catalyst (see page 90), accelerating the series of intermediate reactions involved but without being used up in the process.

[1] The calory is the unit of heat and is defined as the amount of heat necessary to raise the temperature of a gram of water from 3.5° C. to 4.5° C.

Chemical Changes. — The steps in the series of reactions have not been worked out in detail, but two stages seem certain: the reduction of carbon dioxide and water to form formaldehyde and free oxygen ($CO_2 + H_2O \rightarrow CH_2O + O_2$), and the condensation of six molecules of **formaldehyde** to form glucose ($6\ CH_2O \rightarrow C_6H_{12}O_6$).

The by-product oxygen is given off in exactly the same amount as the carbon dioxide consumed, thereby assisting in maintaining the oxygen content of the atmosphere, 20.8 per cent by volume.

A computation by Ganong shows that 25 square meters of green leaf surface on a warm, sunny summer day will liberate as much oxygen as a man will use in respiration during the same period.

Formaldehyde is very poisonous even in low concentrations, but it is condensed into sugar as rapidly as possible under the

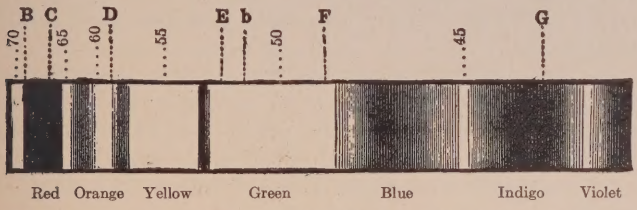

FIG. 43. — Absorption spectrum given by light passing through a solution of chlorophyll. The numbers represent the wave length in hundred-thousandths of a millimeter. (After Kraus, from Holman and Robbins.)

catalytic influence of certain cell enzymes. This reaction is affected by temperature, which therefore affects the rate of the entire photosynthetic process.

End-products. — The end-products of the processes initiated by photosynthesis are the more complex sugars, starches, lipins, and proteins which derive their nitrogen from the soil. These substances, however, can be made by the leaves in darkness as well as by other organs of the plant, and are not dependent upon the radiant energy of the sun, which indeed appears necessary only for the original reduction.

The wheat plant manifests the phenomenon of photosynthesis, or the building up of carbohydrates, lipins, proteins (and presumably vitamins) from inorganic compounds, as its method of preparing food, while the animal shows in contrast the phenomenon of digestion by means of which plant and animal tissue are

broken down into simple carbohydrates, lipins, and proteins capable of being absorbed and circulated.

Respiration. — But like the animal the plant respires, giving off carbon dioxide and taking in oxygen, exactly the reverse of the exchange taking place in photosynthesis. Respiration, however, is not solely a function of the leaf, but may take place in any green region of the plant. Ordinarily during the daylight hours, photosynthesis is more active than respiration, but during weak illumination there may be no gaseous exchange with the atmosphere, as the carbon dioxide liberated in respiration may be just enough to supply the amount required for photosynthesis. At night the plant consumes oxygen and gives out carbon dioxide, as in the respiration of animals.

The existence of respiration indicates that oxidative processes are taking place within the plant and that, as in the animal, potential energy is being transformed into the kinetic energy required for all the activities of the plant, with the sole exception of photosynthesis.

In the metabolism of the plant as a whole the constructive processes far exceed the destructive processes, so that raw materials are being built up into the plant body or stored far more rapidly than the body material is being consumed. The plant then grows rapidly, with limits imposed only by the length of its life and the stores of raw material available in the air and the soil.

RESPONSE TO STIMULI (TROPISMS)

Although the plant has no power of locomotion, the growth of the wheat manifests certain responses to stimuli of various kinds by changes of direction which are called **tropisms.** Thus the root grows in the direction of gravity, the shoot in the opposite direction (Fig. 44). The stimulus is gravity, so that the root is said to be positively **geotropic,** and the shoot is called negatively geotropic. Conversely, the root grows away from the light, the shoot grows toward it (Fig. 45). In this case the root is negatively **phototropic** and the shoot is positively phototropic. The root system tends to grow toward the part of the soil with the higher water content, a phenomenon known as positive **hydrotropism.** Other recognized tropisms are **chemotropism** with respect to chemical stimuli, **thermotropism** due to changes in temperature, and **thigmotropism** in which case mechanical contact is the exciting stimulus.

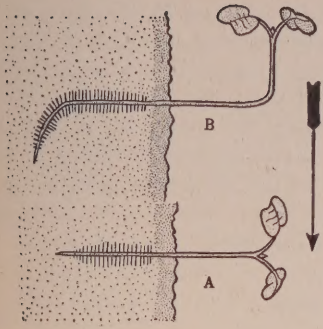

FIG. 44. — Geotropism in mustard seedling. A, when first placed in horizontal position; B, 24 hours later. Arrow indicates direction of gravity. (After Sachs, from Holman and Robbins.)

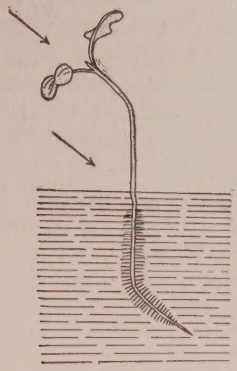

FIG. 45. — Phototropism in mustard seedling, grown in water. The arrows indicate the direction of the light. Note that the shoot is positively phototropic while the root shows negative phototropism. (After Sachs, from Holman and Robbins.)

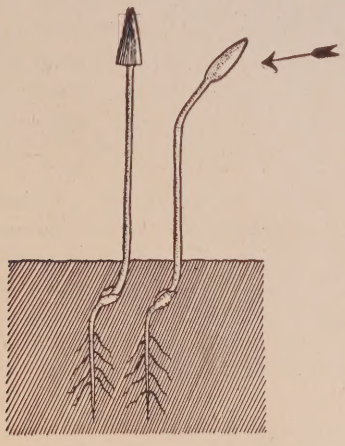

FIG. 46. — Diagram to show transmission of excitation in millet seedlings. The arrow indicates the direction of light. Note that the reception of the stimulus occurs at the tip of the shoot (shaded by a paper cap in the seedling to the left) while the response or bending takes place at a lower level. (After Sachs, from Holman and Robbins.)

The wheat has no sensory-neuro-muscular complex, but irritability must exist, as seen by the tropic responses just described. A degree of transmission is indicated by the fact that young seedlings which evidence a positive phototropism do so by curving toward the light. The region of curvature is some little distance below the terminal bud, but if the bud be shaded by a little opaque cap (Fig. 46), even though the region where curvature should take place is illuminated, there is no response. In this case the light stimulus is received by the terminal bud and transmitted through the stem for a short distance to a region where the response is affected by local growth.

REPRODUCTION

The appearance of the flower marks the onset of the period which may be called that of sexual maturity, for the flower is the reproductive organ of the plant. The flower is essentially a stem without internodes, whose appendages, closely crowded together and without axillary buds, arise from a meristem which is completely consumed in the process of organ formation.

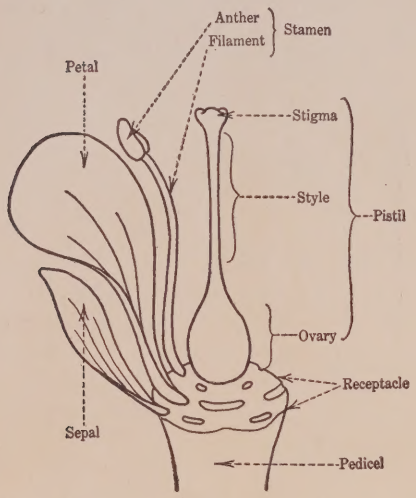

FIG. 47. — Diagram to show the parts of a generalized flower. All but one element of each whorl have been removed. (After Hall, from Holman and Robbins.)

Genital Organs (the Flower). — The flower of the wheat is specialized in so many respects that we shall first examine a more generalized flower (Fig. 47). This consists of a **pedicel** or stem, expanding into a **receptacle,** on which are arranged four whorls of appendages. The outermost (lowest) of these is composed of **sepals** or leaves which have a protective function while the flower is still a bud. Next, within and above this, are the **petals,** which are often large, colored, perfumed and

sweetened leaves. The nectar is a product of glands at the base of the petals. It is the petals which serve to attract the insects whose activities are necessary for the reproduction of many plants. The next whorl contains the male elements, organs called **stamens,** each of which is composed of an **anther** upheld by a narrow **filament.** The innermost ring is represented by the **pistil** arising from one or more **carpels.** The pistil is composed of a basal **ovary** and a **style** extending from it which supports an expanded **stigma.** This may secrete a sweet and sticky stigmatic fluid.

Inflorescence of the Wheat. — The flower of the wheat is a unit of an **inflorescence** or compound flower. This is made up of many small groups called **spikelets** (Fig. 48). A large number of spikelets arise from a common stem or **rachis** to form a **spike,** and these in turn branch from the main axis of the entire inflorescence which is called a **compound spike.**

The spikelet is attached to the rachis by a short axis, which bears a number of chaffy overlapping leaves. Those of the lower rank are called **glumes** and enclose the rest of the spikelet. Those in the upper rank are associated in pairs, of which the outermost is called the **lemma** and the innermost is known as the **palea.** *Each such pair encloses a single flower.*

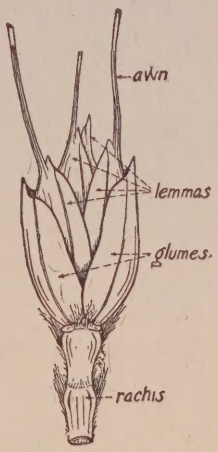

FIG. 48. — *Triticum* spikelet. (From Holman and Robbins.)

The flower has no sepals or petals and consists of a pistil composed of two carpels, three stamens and two scale-like structures which may represent vestiges of petals or sepals. When temperature conditions are favorable, the lodicules swell and force the lemma and palea apart so that the stamens and the two feathery stigmas of the carpels may protrude.

The Pollen. — The anthers consist of two lobes running lengthwise and united by a connective band. Each lobe contains two longitudinal **pollen sacs.** These pollen sacs receive their name from the fact that each contains a great number of tiny pollen grains when the flower is mature. The pollen grains are not gametes comparable to the sperm of the frog, however, although they arise from mother cells by means of two divisions essentially

similar to the maturation divisions of the animal spermatocyte. They are asexual germ cells or **microspores** which have enlarged and secreted a spore wall of two membranes, the inner **intine** and the outer **exine.** Within this wall the **nucleus** (see page 83) of the cell divides to form two daughter nuclei, the **tube** nucleus and the **generative** nucleus. The cell itself does not divide.

Pollination. — When the mature pollen grains are to be shed, the pollen sacs open and the pollen grains are scattered. Many fall

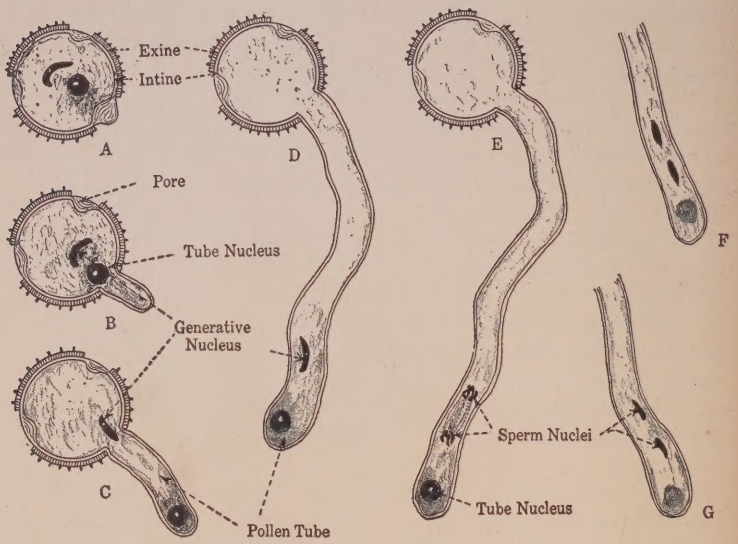

FIG. 49. — Stages in the development of the pollen tube, following pollination. (After Bonnier and Sablon, from Holman and Robbins.)

on the stigmata of the pistils in the same inflorescence, thus bringing about self-pollination. Others may be carried by the wind to the pistils of other plants and cause cross-pollination.

In other flowering plants pollination is brought about by the visits of insects, particularly bees. These insects, attracted by the flowers, remain to gather pollen or nectar. When they fly to another flower some of the pollen grains adhering to their bodies are rubbed off on the stigmata of the second plant. Even self-pollination is impossible in some of the highly specialized flowers

like the orchids unless accomplished through the intervention of insect visitors.

The pollen grain, on coming in contact with the stigma, absorbs water from the stigmatic fluid. Swelling, it ruptures the exine and, surrounded only by the intine, it protrudes through the opening to form the **pollen tube.** The generative nucleus now divides once more, giving rise to two **sperm** nuclei. The pollen tube with its three nuclei is known as the **microgametophyte** because it represents a degenerate sexual plant reduced to its lowest terms. It is composed of the two sperm nuclei each representing a single male germ cell (**microgamete**) and the tube nucleus which with the remaining contents of the tube represents the body of the plant.

The Ovule and Embryo Sac. — The pistil of each flower arises from two carpels, presumably, as it possesses two styles and stigmata. Its ovary is made up of a wall or **pericarp** in which may be distinguished the epidermis, parenchyma, and **chlorenchyma,** a type of parenchyma containing chloroplasts, and a cavity in which is found the **ovule** (Fig. 50). This arises as a protuberance, the **nucellus,** from a region known as the **placenta.** Around it two folds of tissue are formed which unite at the outer end of the nucellus to form the **integuments.** At the very tip, however, they remain separate to leave a small aperture called the **micropyle.**

Within the nucellus one of the cells enlarges to become a mother cell. It then divides twice, thus giving rise to four potential **megaspores** arranged in a longitudinal row. Of these the one nearest the placenta enlarges still more and will become the **embryo sac.** The others collapse and degenerate, reminding us of the two maturation divisions of the animal oöcyte and the subsequent degeneration of the polar bodies.

The megaspore, however, like the pollen grain, is not a gamete, as is shown by its further development. Its nucleus divides and the two daughter nuclei move apart, one towards the micropyle, the other towards the placental end of the cell. Each of these nuclei divides twice to form four micropylar and four placental nuclei. A single member from each group moves towards the center of the cell. These two are thereafter known as **polar** nuclei. The remaining members of the placental group undergo further divisions resulting in the formation of six to eight **antipodal** nuclei. One of the micropylar group becomes the **egg** nucleus, while the others are called **synergid** nuclei. The embryo sac is

now the fully developed **megagametophyte,** a degenerate sexual plant in which the egg nucleus represents the female gamete or **megagamete,** while the remaining ten to twelve nuclei with the other contents of the sac represent the body of the plant.

Fertilization. — The pollen tube is formed soon after the pollen grain has fallen upon the stigma. It penetrates the tissue and makes its way down the style into the ovary. Entering the

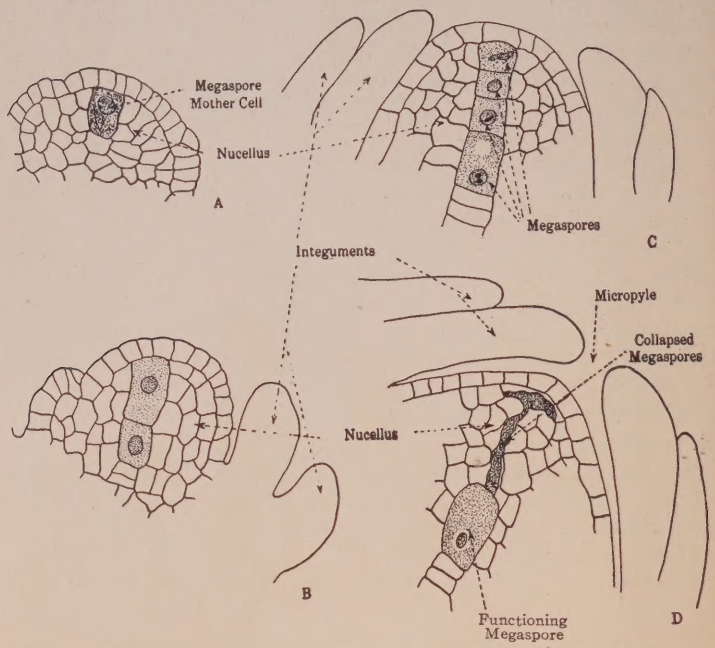

FIG. 50. — *Triticum,* stages in the development of the megaspore, from median lengthwise sections of ovules. (After Percival, from Holman and Robbins.)

micropyle, it penetrates the nucellus and finally reaches the embryo sac. The tip of the tube is then ruptured (Fig. 51), and one of the sperm nuclei fuses with the egg nucleus to form the zygote nucleus. This is comparable to the fertilization of the frog's egg. The other sperm nucleus unites with the two polar nuclei to form the primary **endosperm** nucleus. This is known as double fertilization. The process is completed during the second day following pollination.

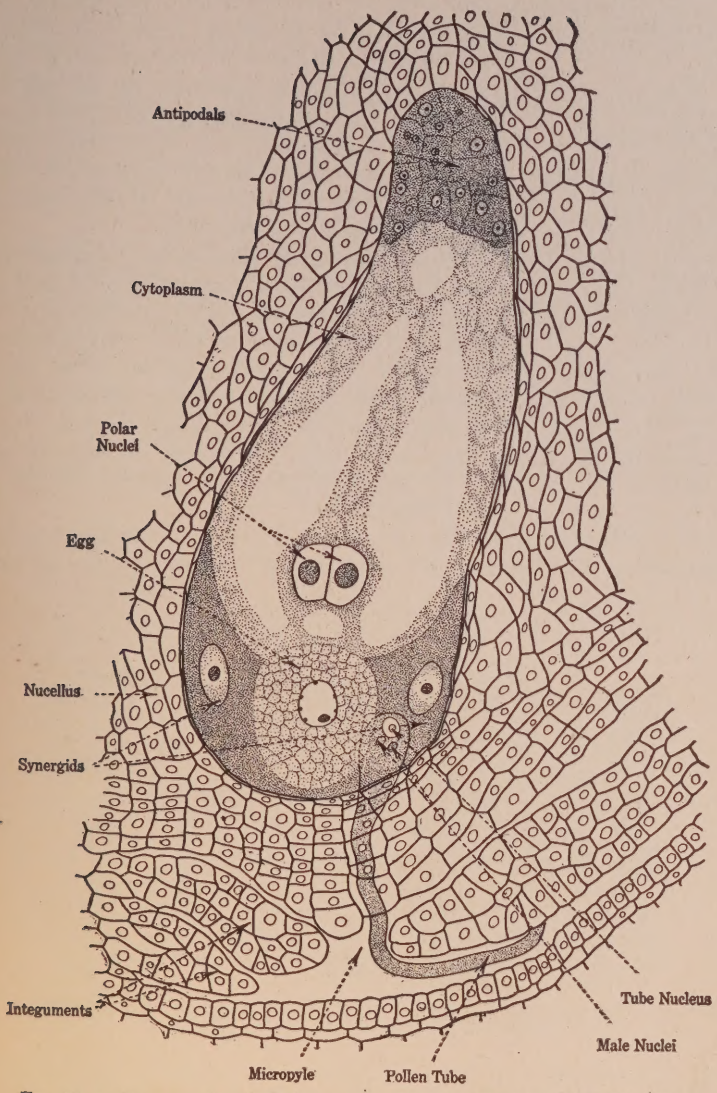

FIG. 51. — *Zea mays* (corn), embryo sac and pollen tube just prior to fertilization. Longitudinal section. (After Miller, from Holman and Robbins.)

The Embryo (Fruit and Seed). — The matured ovary including the ovary and any other flower parts associated with it form the fruit, which in the case of wheat is the grain (Fig. 52). The ovule gives rise to the seed. The ovary wall or pericarp of the wheat is reduced to a relatively thin layer firmly attached to the seed. The **awn** or brush of the wheat develops from the end of the ovary formerly occupied by the style.

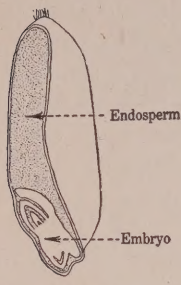

FIG. 52. — *Triticum*, grain in longitudinal section. Note position of embryo. (From Holman and Robbins.)

Within the ovule the inner integument gives rise to the seed coat, while the outer integument disappears. The nucellus is reduced to a single layer of cells. Within the embryo sac the synergid nuclei were destroyed by the entrance of the pollen tube, and the antipodal nuclei disintegrated after serving for a time apparently in absorbing food for the developing embryo from the placental region.

The Endosperm. — The primary endosperm nucleus which arises from the fusion of the polar nuclei with one of the sperm

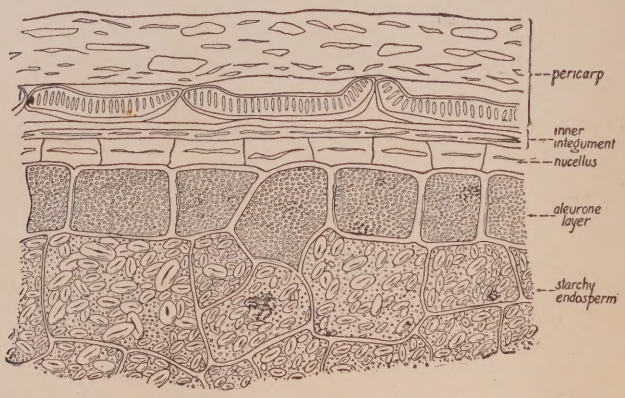

FIG. 53. — *Triticum*, grain in cross section. (From Holman and Robbins.)

nuclei divides repeatedly, and the daughter nuclei fill the embryo sac except for the space occupied by the embryo. Each of these nuclei finally becomes the center of an endosperm cell. This endosperm makes up the greater part of the seed (92 per cent by

volume) and is divided into an outer **aleurone** layer containing some protein constituents, and the inner starchy **endosperm** which may be considered as food stored for the developing embryo.

The Embryo. — The zygote nucleus becomes the center of a cell which divides unequally to form a larger **suspensor** cell

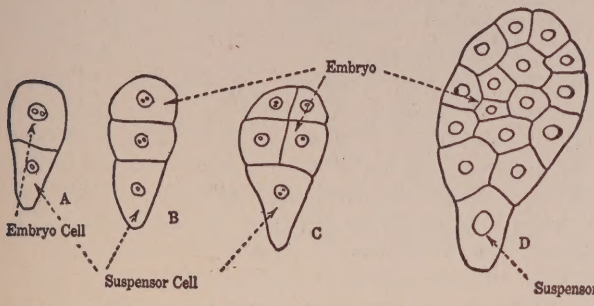

FIG. 54. — *Triticum*, young embryos in longitudinal sections. (After Percival, from Holman and Robbins.)

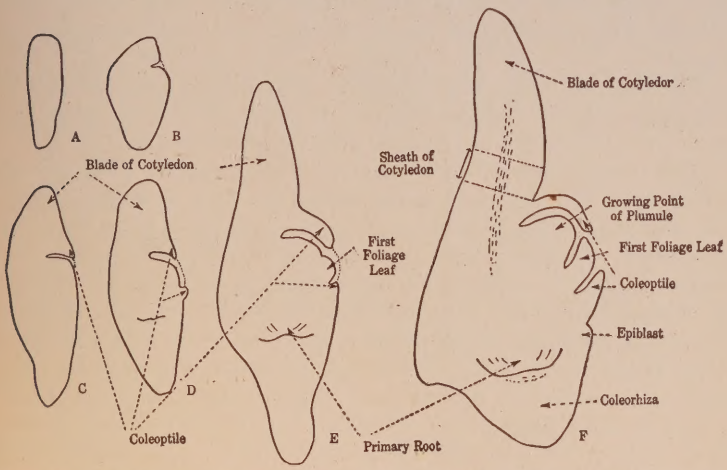

FIG. 55. — *Triticum*, later embryos in longitudinal sections. Outlines only. (After Percival, from Holman and Robbins.)

and a smaller embryo cell. The first is in contact with the wall of the embryo sac, and the second divides repeatedly to form the early embryo. The latter after continued growth by cell

division gives its first evidence of differentiation in the appearance of a lateral groove. The tissue above this becomes the **cotyledon,** a specially modified seed leaf which absorbs food from the endosperm. Below this is the growing point of the **plumule,** the primordium of the shoot, which is surrounded by a modified leaf sheath known as the **coleoptile.** Still further below the **radicle** or primordium of the root appears, with its surrounding root sheath, the **coleorhyza.** The embryo now occupies the end of the seed opposite that of the awn.

Germination. — In this condition the activities of the plant are halted until resumed by germination. The seed, then, is essentially a young plant arrested in its development and surrounded by reserve food materials and protected by seed coats. In this dormant stage the seed may remain for long periods, although delicate tests reveal the fact that respiration is still taking place. Wheat retains its vitality for about two years, after which the ability to germinate or resume growth diminishes. At the end of the first year, for example, 80 per cent of the seed will germinate, while at the end of six years only about 6 per cent will do so. The seeds of some other plants may retain their vitality for two hundred years, which is probably a maximum figure.

The beard of the wheat serves as an attaching organ by which the grain may be transported on the hairs of animals and thus aid in the dispersion of the seed prior to germination.

This resumption of the vital activities requires a supply of water to soften the seed coats, cause the seed to swell, supply the water lost during ripening, permit of respiration, enzyme formation, digestion, and the transfer of materials within the seed. Oxygen is required for respiration, as the seed is incapable of photosynthesis and consumes its own stored food by oxidation, liberating chemical energy as heat, and giving off carbon dioxide. Over 50 per cent of the dry weight is lost in the process. Digestion is carried on by means of enzymes comparable to those found in animal digestion. Circulation is by diffusion gradients. The temperature limits for the germination of wheat are between 5° and 42.5° C., with an optimum temperature of 29°.

The Seedling. — In germination the primary root breaks through the coleorhyza and the seed coats and soon produces the lateral roots of the temporary root system. The plumule emerges from the opposite end, and the first foliage leaf soon breaks though the coleoptile. The cotyledon does not emerge from

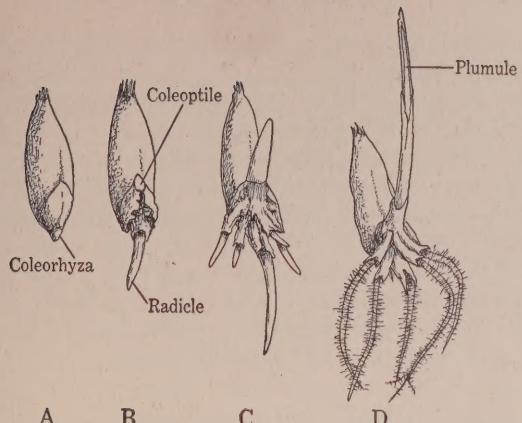

FIG. 56. — *Triticum*, stages in germination of the seed. (After Bocquillon.)

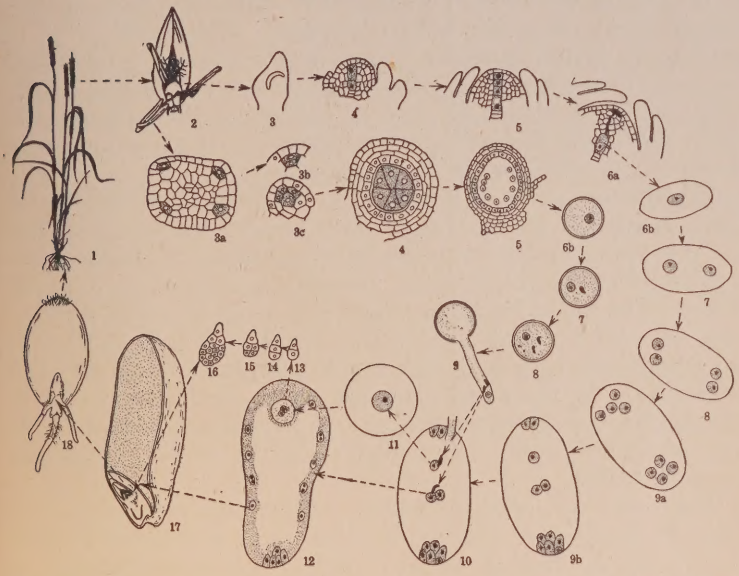

FIG. 57. — *Triticum aestivum*, life history. 1, mature sporophyte; 2, single flower; (outer circle) 3–6b, development of megaspore; (inner circle) 3–6b, development of microspore; (outer circle) 7–9b, development of female gametophyte or embryo sac; (inner circle) 7–9, development of male gametophyte or pollen tube; 10, fertilization; 11, zygote; 12, zygote and endosperm in embryo sac; 13–16, stages in development of sporophyte; 17, mature grain with embryo; 18, germinating grain. (From Holman and Robbins.)

the seed, but remains in contact with the endosperm and serves as an absorbing organ to pass on the reserve nutriment to the developing embryo. Chloroplasts appear in the stem and its leaves, and the photosynthetic activities of the plant are inaugurated. New adventitious roots arising at the base of the first foliage leaf replace the primary roots derived from the radicle, and branch stems (tillers) appear. With the onset of photosynthesis the period of germination may be considered ended, and the young seedling soon assumes the characteristic habit of the sporophyte, as the asexual generation is called to distinguish it from the degenerate sexual gametophytes represented by the pollen tube and the embryo sac.

COMPARISON OF PLANT AND ANIMAL ACTIVITIES

In spite of the obvious dissimilarities between a frog and the wheat plant, they are both organisms. What have they in common? Both require food which they subject to complicated chemical changes involving the transformation of energy. Both respond to stimulation effected by changes in the environment. Both reproduce themselves by detaching portions of their own bodies from which new individuals develop.

Metabolism. — The frog is unable to build up its food from raw materials but is able to break down (digest) the complex compounds found in the bodies of other organisms to simpler compounds which can be absorbed and circulated to all parts of the body. The wheat is able to absorb water and mineral salts from the soil and to conduct them by transpiration to the leaves where they are combined with carbon dioxide absorbed from the atmosphere to form carbohydrates, lipins, and proteins. The initial step, the combination of carbon dioxide and water to form glucose in the presence of sunlight (photosynthesis), is peculiar to green plants.

Both frog and wheat consume oxygen and give off carbon dioxide (respiration) due to the oxidation of substances in their bodies which liberate energy. This respiratory exchange is greater in the frog because of its locomotor activity. Other waste products including the nitrogenous and inorganic compounds are given off (excreted) by both frog and wheat, but again in greater quantities by the former.

Both have conducting systems. That of the frog (blood vascular system) is a closed circulating system in which a special-

ized tissue, the blood, serves as a common carrier, pumped around by the heart. In the conducting system of the wheat (vascular bundles) the common carrier is the sap, water which is drawn up through the xylem by root pressure and transpiration, and descends in the phloem under the influence of gravity.

Irritability. — The locomotor activities of the frog are carried on by a sensory-neuro-motor complex which is not represented in the wheat. The latter is anchored to the soil by its roots. The prime activity of the plant is growth, which takes place at or near the ends of the organ and continues throughout life. Its sole tropic response to environmental stimuli consists in changing the direction of growth, a phenomenon which indicates reception, transmission, and reaction, although no special structures for these functions are developed. The growth of the frog is not confined to the extremities and ceases soon after sexual maturity.

Reproduction. — The development of the frog is initiated by sexual reproduction. That of the plant involves the alternation of both sexual and asexual generations. In both wheat and frog the production of gametes is preceded by two maturation divisions.

Structure. — In examining the structure of these two organisms, unlike as they are, it has been necessary to speak of organs, such as the heart of the frog and the leaf of the wheat. These organs we found to be composed of tissues, such as the mucosa of the frog's intestine or the xylem and phloem of the vascular bundles in the wheat. Tissues are composed of cells, which appear to be the ultimate architectural units of both the frog and the wheat. In particular we noted that both the frog and the wheat sporophyte originate from a single cell, the zygote, and that this in turn arises from the fusion of a microgamete and a megagamete, sperm and egg, respectively. Let us now turn our attention to the cell and its activities in metabolism, irritability, and reproduction.

CHAPTER IV

THE CELL AND METABOLISM

The study of the structure and activities of a plant and of an animal has shown us how impossible it is to discuss these subjects without constant reference to the cell, for modern Biology is founded upon the cell theory. But the discovery of cells waited upon the invention of the microscope, which was achieved about 1590 by the Janseen brothers, makers of spectacles in

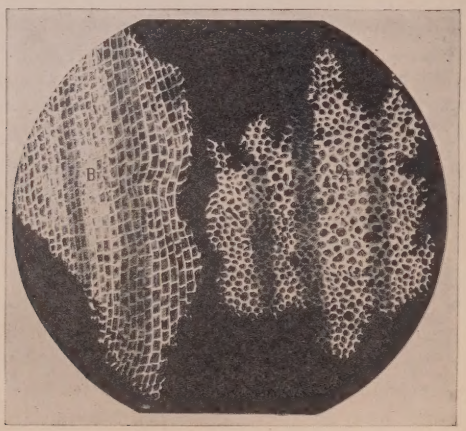

FIG. 58. — The first picture of cell structure. (From Hooke's illustration of cork, in Holman and Robbins.)

Middleburg, Holland. In 1665 an English microscopist, Robert Hooke, published his discovery that cork when magnified was composed of numerous tiny and empty compartments to which he gave the name cells (Fig. 58). Owing, we suppose, to the imperfections of his microscope, he overlooked the contents of these cells in living material, and it was not until 1772 that it was reported that the cells of living plants were not empty. The cell nucleus was seen and figured in 1781 but it was not recognized as an important and universal part of the cell until 1833. The

universal occurrence of cell structure in plants and animals was the discovery of Schleiden (1838), a German botanist, and of Schwann (1839), a zoölogical colleague, who jointly arrived

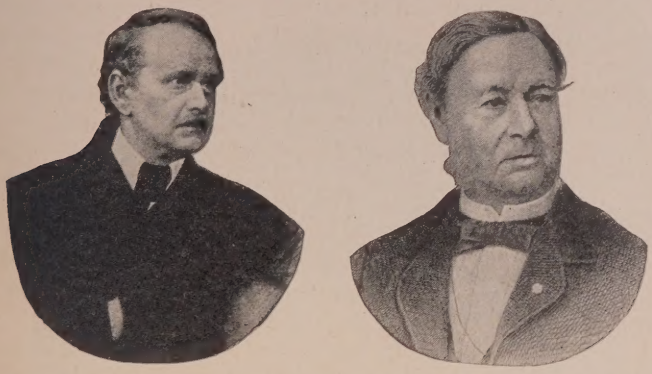

FIG. 59. — Matthias J. Schleiden, 1804–1881 (on left); Theodor Schwann, 1810–1882 (on right). (From Locy, "Makers of Biology," Henry Holt and Co.)

at the conclusion that the "universal principle of development for the elementary parts of organisms . . . is the formation of cells" (Schwann). These founders of the cell theory did not, however, recognize the importance of the fluid cell contents.

PROTOPLASM

Dujardin (1835) described the contents of the cell wall in single-celled animals, Protozoa, while von Mohl (1846) described a similar substance in plant cells which he called **protoplasm.** Max Schultze (1861) discovered the same substance in the cells of the more highly organized animals and enunciated the theory that the protoplasm of all cells, simple or complex, plant or animal, is basically identical. He defined the cell as a mass of protoplasm, including a nucleus and surrounded by a membrane.

Chemical Constituents. — Many attempts have been made to analyze the chemical structure of protoplasm, but in vain, and the modern conception of the term is a state of chemical and physical activitiy in a mixture of many different chemical compounds. The essence of protoplasm is the activity rather than the mixture, for when the cell is killed the protoplasm becomes a mass of decomposing compounds.

Elements. — Nearly all of the chemical elements have been identified in protoplasm but of the 92 known elements, only 12 are commonly found: carbon, oxygen, hydrogen, nitrogen, sulphur, phosphorus, potassium, sodium, calcium, magnesium,

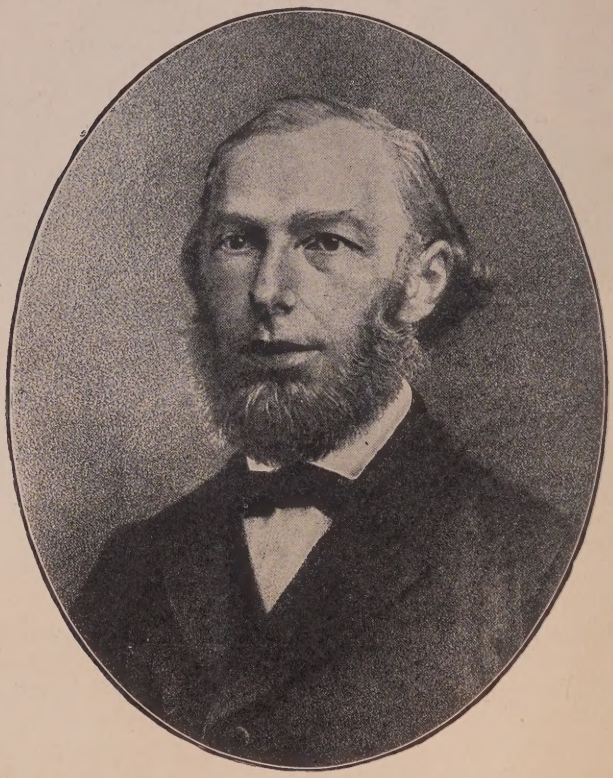

FIG. 60. — Max Schultze, 1825–1874, who established the universality of protoplasm. (From Locy.)

iron, and chlorine. Ninety-nine per cent of protoplasm by weight is made up of carbon, oxygen, hydrogen, and nitrogen.

Compounds. — The most common of all the chemical compounds found in protoplasm is water, which makes up from 70 to 90 per cent of its weight. As a solvent it contains inorganic salts and gases in solution, as well as many of the organic com-

pounds. It also enters into most of the chemical reactions which take place within the cell (metabolism), either dissociating into its constituents, the hydrogen ion (**H**) and the hydroxyl ion (**OH**), or combining from these.

The inorganic salts are combinations of the electropositive ions (**anions**) potassium (**P**), sodium (**Na**), ammonium (NH_4), calcium (**Ca**), magnesium (**Mg**), and iron (**Fe**), with the electronegative ions (**cations**) chloride (**Cl**), sulphate (SO_4), nitrate (NO_3), nitrite (NO_2), carbonate (CO_3), bicarbonate (HCO_3), and phosphate (PO_3, HPO_4, or H_2PO_4). The salts are usually found dissociated into their constituent ions which may combine to form acids (cations and hydrogen ions), bases (anions and hydroxyl ions), or as salts (anions and cations). If there are more hydrogen ions present than hydroxyl ions, the solution is acid; if these are equal in number, the solution is neutral; if the hydroxyl ions predominate, the solution is basic. Protoplasm is almost exactly neutral.

The gases present are oxygen (O_2), carbon dioxide (CO_2) and ammonia (NH_3). The last-named, however, is rapidly transformed into other compounds.

The Organic Compounds. — The characteristic compounds found in protoplasm are the organic compounds, so called because they do not exist under natural conditions save as the product of the metabolism of organisms. Organic compounds are made up of carbon and hydrogen, with the hydrogen often replaced by atoms of other elements or by radicles (submolecular atomic groups). The peculiarities of these organic compounds are due to the presence of the carbon atom, which is able to combine with other atoms of carbon to form long chains, rings, or chains of rings. These are skeletons to which are attached other atoms and molecules. In this way molecules containing thousands of atoms with complex structure may be built up. The three great groups of organic compounds which have been found in protoplasm are the carbohydrates, lipins, and proteins.

Carbohydrates. — The carbohydrates are compounds of carbon, hydrogen, and oxygen in which the proportion of hydrogen atoms to those of oxygen is the same as in water (H_2O). The carbon atoms are arranged in chains of six atoms each. The single-chain compounds are called simple sugars (**monosaccharoses**), e.g., **glucose** ($C_6H_{12}O_6$). This, it will be recalled, is the formula of the sugar which the plant cell photosynthesizes from CO_2 and H_2O. Ordinary cane sugar (**sucrose**) has twelve carbon atoms

and is called a **disaccharose.** These sugars are very soluble in water. The more complex sugars are known as **polysaccharoses** and include such compounds as the starch of plant cells, the glycogen of the animal cell, and the cellulose which forms the wall of the plant cell. They are insoluble in water or nearly so.

Lipins. — The lipins are compounds of carbon, hydrogen, and oxygen, in which the ratio of oxygen to hydrogen is less than in the carbohydrates; they are generally characterized by their greasy nature. They are insoluble in water but go into solution in various organic liquids, particularly in ether and chloroform. Examples are the true **fats** composed of **glycerine** and **fatty acids,** e.g., butter fat and olive oil; the **phospholipins** which contain phosphorus, e.g., **lecithin,** found in egg yolks; and the **waxes.**

Proteins. — The proteins are compounds of carbon, hydrogen, oxygen, and nitrogen. They range in complexity from the simple amino-acids, that is to say, organic acids containing the amine radicle (NH_2) and the carboxyl radicle (**COOH**), up to such molecules as that of **casein** found in milk which has over 20,000 atoms. This group is the largest and contains the most complex organic compounds.

Metaplasm. — In protoplasm the various components are being rearranged continuously in the chemical and physical activities of life. Certain compounds are stored as food reserves, excreted as waste, or utilized as by-products in the formation of supporting or protective structures inside or outside the cell. When found within the cell they are distinguished from the protoplasm proper under the general term of **metaplasm.**

Physical Structure. — Protoplasm generally presents the appearance of a slow-flowing liquid, transparent and colorless. Its various reacting compounds are dissolved or suspended in water, which makes up the greater part of the system. It is not, however, an ordinary solution, for many of the components are present as extremely small bubbles of gas, droplets of water, or as solid particles. A system in which the medium or **continuous phase** is a liquid while the particles, known as the **dispersed phase,** are larger than the ions or molecules of the ordinary type of solution, is called a **colloid** solution, and many of the phenomena of protoplasm are being investigated in terms of colloid chemistry.

Viscosity. — One of the peculiarities of protoplasm is its tendency to undergo changes in viscosity, that is, its ability to change from a less viscous (**sol**) condition to a more viscous (**gel**) condition, and vice versa. Such changes have been demon-

strated in cell division and during the fertilization of the egg. Such reversals of phase are well known in colloid solutions of the **emulsion** (liquid-in-liquid) type. When in churning cream, which is an emulsion in the sol condition, with fine droplets of butter fat, constituting the disperse phase, and water, making up the continuous phase, we obtain butter, the result has been a reversal of phases in which the dispersed phase consists of droplets of whey (water, etc.) and the continuous phase is butter fat, while the system is in the gel condition.

The enormous variety of reactions taking place among the components of protoplasm is facilitated by the dispersion of these compounds and the consequent increase of surface between the various phases concerned.

CELL STRUCTURE

The cell is the structural unit of protoplasm. All plants and animals have a cellular organization, whether the organism is in the form of a single cell, such as the unicellular plants and animals (**Protophyta, Protozoa**), or is composed of many cells (**Metazoa, Metaphyta**). We have seen many different types of cells in the tissues of the frog and of wheat, but all have some structures in common, which we may put together in an ideal or generalized type of cell (Fig. 61).

Membranes. — The cell always has a **plasma-membrane,** which is simply the surface layer of the protoplasm, differentiated from the rest of the cell by the fact that it is that part of the cell which is in actual contact with the environment. Outside the plasma-membrane are other cell walls which are by-products rather than part of the protoplasm. Most plant cells are surrounded by a cell membrane of cellulose, an insoluble carbohydrate (polysaccharose). The exine and intine of the pollen are other examples. Cartilage and bone are largely fused cell membranes. The vitelline membrane of the frog's egg is still another type of cell membrane.

The Nucleus. — The protoplasm of the cell inside the plasma-membrane consists of the **karyoplasm** inside the nucleus, and the **cytoplasm** outside the nucleus. The two are separated by the nuclear membrane, concerning the origin of which we are still uncertain. It may be the inner layer of the cytoplasm or the outer layer of the karyoplasm. In either case it is apparently a semipermeable membrane (see page 93) between the two.

The karyoplasm is best studied in cells which have been prepared for microscopic examination by killing them, slicing them extremely fine, staining the slices with dyes which react differently to acids and bases, and mounting them in penetrating liquids with a high refractive index. It is characterized by the presence of **chromatin,** small granules which undergo an intense staining reaction with basic dyes. They form linear aggregates called **chromosomes** when the cell divides. We shall have

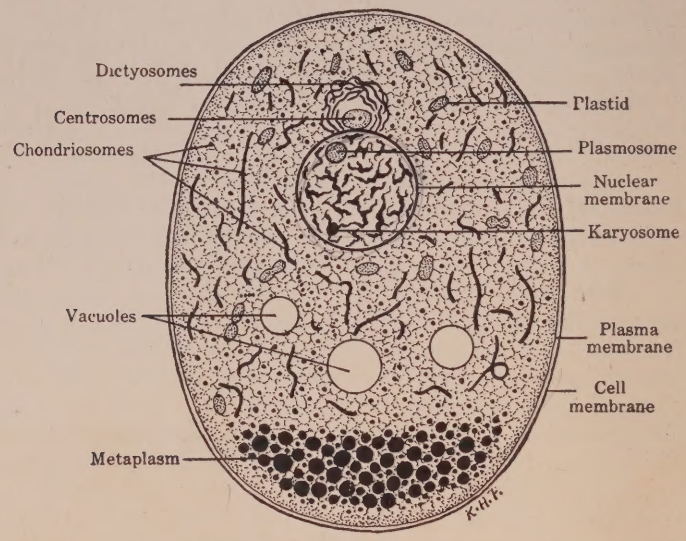

FIG. 61. — Diagram to show the anatomy of a generalized cell. Compare Figs. 62 and 63. (After Wilson, from Shumway.)

occasion to refer to these chromosomes frequently in coming chapters, as they are intimately concerned with the transmission of hereditary characters from cell to cell and from generation to generation. Two types of bodies known as **nucleoli** are found in the nucleus: the **karyosome,** which reacts to basic dyes, and the **plasmasome** which is stained by acid dyes.

The nucleus seems to be the center of the internal activities of the cell. The most striking difference between the karyoplasm of the nucleus and the cytoplasm is the presence of chromatin in the former. In cells prepared for microscopic examination this substance appears in the form of granules. It is interesting

to note in this connection that some of the unicellular organisms, e.g., bacteria, do not have a typical nucleus. Their chromatin is scattered about in the protoplasm as granules (**chromidia**). When a cell is about to divide, the chromatin granules arrange themselves in long thin bodies, the chromosomes. The study of Heredity (Chapter VII) shows that these chromosomes are linear aggregates of unlike particles called **genes.** These are too small for even microscopic observation ($6 \cdot 10^{-6}$ cm. estimated diameter), but they are responsible for the transmission of all hereditary characteristics from one generation to another, and therefore for all the internal factors of cellular activity.

Enucleate Cells. — If certain protozoa are cut in pieces in such a way that one piece has the nucleus and the other is **enucleate,** the first portion is able to reorganize itself to its original form, grow, and reproduce itself. The enucleate fragment, however, while it may move about and respond to stimuli, is like a machine gradually running down. It uses up its own substance, principally by oxidations, and eventually dies. The red blood corpuscles of mammals are enucleate and therefore incapable of reproducing themselves. Further evidence as to the importance of the nucleus will be presented in the following chapters.

The Cytoplasm and its Inclusions. — The cytoplasm contains a variety of so-called formed bodies which reproduce themselves by division inside the cytoplasm, as well as the cell-inclusions which are passive accumulations of metaplasm.

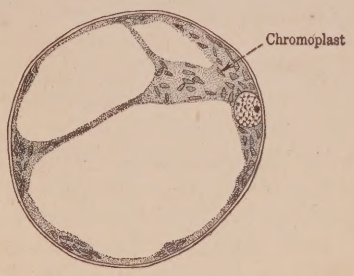

FIG. 62. — Cell from flesh of tomato (*Lycopersicum esculentem*), to show chromoplasts. Note also the large vacuole traversed by strands of cytoplasm, and the nucleus, on the right. (After Frank, from Holman and Robbins.)

Plastids. — **Plastids** are bodies found only in plant cells and a few of the unicellular animals. They are of three types: the colorless **leucoplasts,** the green **chloroplasts** to which we have already called attention as the centers of photosynthesis, and red, yellow, or brown **chromoplasts,** which contain the pigments **carotin** and **xanthophyll.** The same plastid may pass through all three of these stages, as when the colorless leucoplast of the young tomato fruit turns into a green chloroplast and finally a red chromoplast (Fig. 62). So

too the autumnal colors of the leaf are assumed when the chloroplasts lose their chlorophyll and reveal the carotin and xanthophyll hitherto masked.

Chondriosomes. — **Chondriosomes** are minute bodies, granular or rod-shaped. They may be distinguished in the living cell from all other granules because they take on a blue-green tint when the cell is immersed in a dilute solution of a dye called Janus Green B. Different theories have been put forward as to their function. Some think that they are bacteria living within the cell; others hold that they are centers of plastid formation, or are concerned

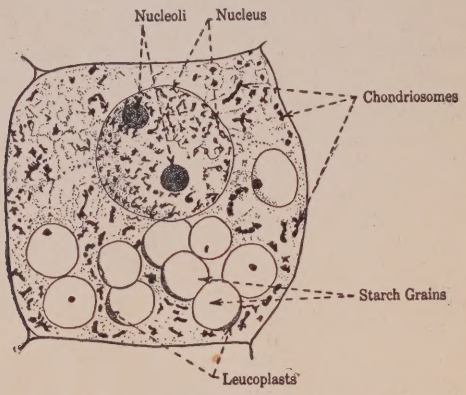

Fig. 63. — Cell from the root of edible pea (*Pisum sativum*), to show chondriosomes. (After Mottier, from Holman and Robbins.)

with the elaboration of the cell inclusions. They have been found in all types of plant and animal cells which have been properly prepared for examination.

Dictyosomes. — **Dictyosomes** are rod- or sickle-shaped bodies found in animal cells which often aggregate near the nucleus to form a net-like structure. This net disintegrates into its component dictyosomes at the time of cell division and is reformed during the reorganization of the cell which follows. The most suggestive of the various theories that have been offered as to their function is that they are concerned in some way with the formation of enzymes.

Centrosomes. — The **centrosomes** are minute granules found near the nucleus in all cells except those of the flowering plants. When found they take part in cell division. In the unicellular

organisms which move by the lashing of a whip-like thread called the **flagellum** (Fig. 64), and in the flagellated sperm of the frog and other animals, the centrosome is connected with the axial filament of the flagellum.

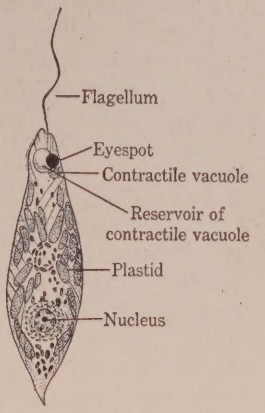

FIG. 64. — *Euglena viridis*, a green flagellate. (After Doflein.)

Metaplasmic Inclusions. — The cell-inclusions which make up the metaplasm include all raw food materials which have not yet entered into the metabolism of the cell, stored food material, by-products, and wastes. These form gas-bubbles, **vacuoles** (droplets of liquid surrounded by a temporary semipermeable membrane), or particles of solids either in crystalline or amorphous form.

The plant cell is characterized by large vacuoles (Fig. 62), in which is found the sap, i.e., water containing in solution gases, salts, and organic compounds. The pigments which cause the color of most blue flowers are found dissolved in their cell sap. Oils and fats form smaller droplets in both plant and animal cells.

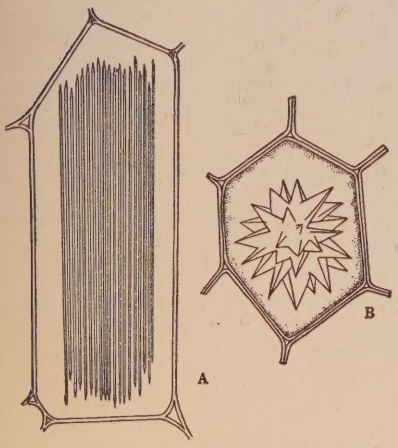

FIG. 65. — Crystals in plant cells; A, *Tradescantia;* B, *Rumex.* (From Holman and Robbins.)

Crystals of calcium oxalate are formed by the plant cell from oxalic acid produced in excretion. In animal cells, crystals of calcium carbonate are sometimes formed, but in general the waste products of animal metabolism are disposed of by excretory organs, and the occurrence of crystals within the cell is a pathological phenomenon.

Plant cells usually contain granules of starch in storage. Glycogen may be demonstrated in some animal cells, particularly the vertebrate liver. The egg of the animal contains plates or

spheres of yolk in storage for the developing embryo. In some forms such as the reptiles and birds the amount of stored yolk far exceeds the amount of protoplasm. In the hen's egg (Fig. 66), the yolk is a sphere about 40 mm. in diameter, while the protoplasm proper forms a thin disc whose diameter is but 4 mm. Both are surrounded by the vitelline membrane which is the cell wall. This in turn is surrounded by the albumen, shell membranes, and shell, which, like the jelly of the frog's egg, are

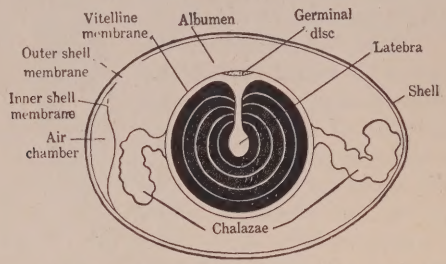

FIG. 66. — Diagram of section through the hen's egg. The protoplasm is represented by the area marked germinal disc. (After Lillie, from Shumway.)

secreted by the walls of the oviduct. Other inclusions represent intermediary stages in metabolism or by-products, such as the pigment granules which give the black color to the upper hemisphere of the frog's egg.

CELL ACTIVITIES

The cell itself is organized and contains bodies called **organelles** (e.g.,the flagellum, etc.) by means of which the various functions of cell life are carried on. We may distinguish two phases in the life of the cell: one is the so-called " resting stage " during which the cell is engaged in maintaining its existence, and the other is the " dividing stage " in which the cell reproduces itself. (See Chapter VI.)

Anabolism and Catabolism. — By the maintenance of the cell is meant all of the activities of the cell except those primarily concerned with reproduction. The existence of the cell depends upon its maintaining a balance between the protoplasm and the environment separated from it by the plasma-membrane. The interchanges of material are manifested by the metabolism of the cell; the interchanges of energy are shown by its irritability.

In the metabolism of the frog, we observed the parts played by digestion, circulation, respiration, excretion, and the endocrines. In the metabolism of the wheat, we noted the phenomena of root absorption, conduction by transpiration, photosynthesis, respiration, and excretion. In the metabolism of the cell, we must consider the intake of material from the environment, absorption, and the discharge of materials to the environment, secretion, both taking place in the plasma-membrane. Within the cell are found indications of many chemical reactions which are either constructive or destructive. The constructive processes are sometimes called **anabolic;** they involve the building up of larger, more complex molecules. As they require the expenditure of outside energy and result in the storing up of potential energy, they are also called **endothermic.** The destructive processes are sometimes called **catabolic;** they involve the breaking down of large complex molecules into smaller and simpler ones. As they liberate stored-up potential energy, they are also called **exothermic.** The term assimilation (page 17) is often applied to the intake and anabolic processes by which the amount of protoplasm is increased while the term dissimilation is applied to the catabolic processes and discharge by which the amount of protoplasm is decreased. There is no reason to suppose that anything other than the same laws as those applying to other physico-chemical systems are involved.

Dissimilation. — The exothermic reactions most frequent in metabolism are **hydrolysis** and **oxidation.** Hydrolysis is sometimes defined as the addition of water. A more exact statement is that the water is dissociated into its component ions, and these unite with ions freed from the compound undergoing hydrolysis, thus producing new compounds. Oxidation, generally defined as the addition of oxygen, often means that in the presence of oxygen, hydrogen ions leave the larger compound to associate with the oxygen in water while the remaining components reorganize themselves in smaller molecules.

Assimilation. — The endothermic reactions corresponding to these are **dehydration** and **reduction.** In dehydration hydrogen ions are removed from one molecule and hydroxyl ions from another; these combine as water while the rest of the molecules unite in a larger molecule. In reduction free oxygen is given off or hydrogen added. The first step in photosynthesis, namely, the combination of a molecule of carbon dioxide (CO_2) and one of water (H_2O) in the presence of chlorophyll and sunlight to form

a molecule of formaldehyde (CH_2O) and one of oxygen (O_2), is an example of the reduction of carbon dioxide.

Many of the other chemical reactions which at first sight appear not to involve these four types probably are the result of simultaneous or alternate oxidation and reduction, or of hydrolysis and dehydration.

Catalysis and the Enzymes. — Most of the chemical reactions which take place in metabolism may be reproduced in the laboratory but not with the same speed or selectivity. Thus in the oxidation of glucose some hundred different chemical compounds may be formed simultaneously. In the living cell few of these occur and these form a regular succession leading to the rapid production of the end-products, carbon dioxide and water.

The speed and specificity of chemical reactions are due to the presence of substances called **catalysts.** At the end of the reaction the catalyst can be recovered in its original quantity, showing that nothing has been lost or used up in the process. The catalyst does not determine the direction of the reaction, which is theoretically reversible, but in the absence of other determining factors always proceeds in the direction by which potential energy is decreased. Thus glucose breaks down into carbon dioxide and water very readily but is built up from these compounds only in photosynthesis. Temperature also affects the speed of chemical reactions, which proceed more rapidly at higher temperatures.

The reactions of metabolism involve the presence of catalysts which are highly specific in their action, effective in extremely minute quantities, and limited in the temperature range of their activity. These are called enzymes. We have already called attention (page 13) to the enzymes concerned with the digestive activities of the frog. These enzymes of the gastric and of the intestinal juices act in the digestive tube to facilitate the decomposition (mostly by hydrolysis) of the carbohydrates, lipins, and proteins passing through. They are formed, however, in the cells of the stomach and intestinal glands, including the pancreas, and discharged through the plasma-membranes of these cells into the tube through the ducts of the glands. Cells which discharge enzymes to be used outside the cell body are called secretory cells. The process of secretion will be discussed below. Enzymes which act as catalysts within the cell body are formed by all types of cells.

The chemical composition of enzymes is unknown, but there is reason to suppose that they are mixtures containing a protein

component because they are destroyed by heat at temperatures running above 60° to 70° C. Enzymes are manufactured within the cell as by-products or intermediate products of metabolism. In this connection it should be recalled that catalysts exist for every chemical reaction, and that, conversely, every chemical compound will act as a catalyst to accelerate some chemical reaction.

Enzymes are divided into **hydrolases** and **oxidases.** Those of the first group accelerate hydrolysis and dehydration in specific reactions. Those which act on carbohydrate hydrolysis are called **saccharases;** those which act on lipin hydrolysis are known as **lipases;** the enzymes which hydrolyze proteins are called **proteases.** The enzymes by which oxidation and reduction are accelerated are called **oxidases.** The same enzymes are often found in both plant and animal cells, as may be seen from the accompanying table of enzymes identified in the wheat seed and in the digestive juices of the frog.

A Partial List of Digestive Enzymes Found in

A. The digestive juices of the frog:	Function:	B. Wheat seeds:
Amylopsin	Starch to maltose	Diastase
Pepsin	Proteins to peptones	Peptase
Lipase	Lipins to glycerine and fatty acids	Lipase
Maltase	Maltose to glucose	Maltase
Trypsin	Peptones to polypeptids	?
Erepsin	Polypeptids to amino-acids	Ereptase

Absorption, Secretion, and Permeability. — The continuance of metabolism requires the intake of new material from the environment (absorption) and the discharge of surplus or waste material to the environment (secretion). These processes take place at, in, or through the plasma-membrane and may be considered as the reverse action of each other. Some writers distinguish secretion from excretion on the ground that secretion involves the discharge of useful material while the products discharged in excretion are waste products. This conception, while helpful in distinguishing the activities of the kidney from those of the pancreas, for example, has little value when dealing with the metabolism of the cell. For the cells of the pancreas and those of the kidney are specialized secretory cells, that is to say, they discharge larger amounts of material through the plasma-membrane than other types of cells. A similar example in the plant kingdom is seen in the specialized secretory cells in the nectaries, the sugar-secreting glands of the flower.

The materials which pass into the cell always do so in solution. Some of the protozoa, like *Paramecium* (Fig. 67) appear to take in solid particles (ingestion), but an examination shows that such solids are always enclosed in a vacuole with a semipermeable membrane. Through this, enzymes are secreted until the contents are in large part made soluble (hydrolysis) and then absorbed through the membrane of the vacuole into the protoplasm. Meanwhile the solid insoluble residue accumulates as an inert mass of metaplasm until it is voided from the cell by the rupture of the cell-membrane (egestion) at a point known as the anus or **cytopyge.** The transfer of gases in respiration is accomplished by the gases going into solution in water and diffusing through the plasma-membrane.

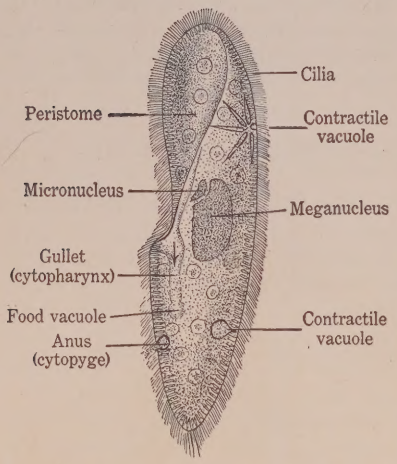

FIG. 67. — *Paramecium caudatum.* Slightly diagrammatic. ×250.

Before continuing with an account of the method of absorption and secretion through the plasma-membrane, it will be well to note a few differences of terminology which the reader will encounter when he turns to botanical and zoölogical texts, for these specialists do not always speak the same language. We have already pointed out that we have used the term secretion to refer to all *discharges* through the plasma-membrane, while others restrict the word to the discharge of *useful* materials such as enzymes and endocrines, and still others use it to refer to the *manufacture* of useful materials for use inside the cell ("intracellular secretion") or outside the cell. We have used the term respiration to refer to the *gaseous* exchange of carbon dioxide and oxygen between the organism and the environment, while some botanists include as well the entire process of the *oxidation* of glucose which involves of course the consumption of oxygen and formation of carbon dioxide. Some zoölogists include the formation of carbon dioxide under the head of excretion, on the other hand, because it is a *waste* product of the animal.

Diffusion. — Both absorption and secretion as the words are used in this text are phenomena of the plasma-membrane. This is what is known as a **semipermeable membrane.** It is well known that substances in solution tend to space themselves equidistantly from each other. Thus if we place a lump of sugar in water, the sugar particles (molecules) move from the region of high concentration to the regions of low concentration until all regions are brought to the same degree of concentration. This phenomenon is known as **diffusion,** and the movements of the particles set up what are known as diffusion **gradients,** that is to say, in the line between the maximum and minimum degrees of concentration, all intermediate grades will be found. The rate of diffusion depends upon the size of the diffusing particles and the nature of the medium in which they are dispersed, and to a slight degree upon the temperature. Larger particles diffuse more slowly and smaller ones more rapidly. In a solid, diffusion is slower than in liquids. Diffusion through a gel is not as rapid as in a sol. Diffusion proceeds most rapidly through liquids in which the particles are soluble. If we form a mental picture of bodies with different sizes and shapes jostling each other through a spongy tissue until the different types are evenly distributed, we shall have a rough idea of the process.

Fig. 68. — Diagram to show diffusion from crystal in water. A line drawn from the crystal to the upper right-hand corner would indicate a diffusion gradient. (From Holman and Robbins.)

Permeability. — Now let us interpose a wall through the spongy tissue. If this wall has no openings or the openings are smaller than the smallest particles in the sponge, it may be called an impermeable membrane, and no diffusion can take place through it. If the wall has a lattice-like structure with openings as large as the largest bodies, it is a permeable membrane, and diffusion will take place almost as though it were not present. But if the openings in the wall are too small to accommodate the largest bodies while large enough for some of the smaller bodies to pass through, then the membrane is semipermeable, and the diffusion of the small bodies will be unhindered and those of the large bodies prevented.[1]

[1] The "lattice," or "sieve," theory is only one of several that have been used in explanation of semipermeable membranes.

Osmosis. — The diffusion of a solvent such as water through a semipermeable membrane is called **osmosis,**[2] and both absorption and secretion are osmotic processes, in which the plasma-membrane acts as the semipermeable membrane. The most common example of osmosis is the passage of water from a solution containing a weak solution of sugar to one containing a strong solution through a membrane impermeable to the sugar molecules.

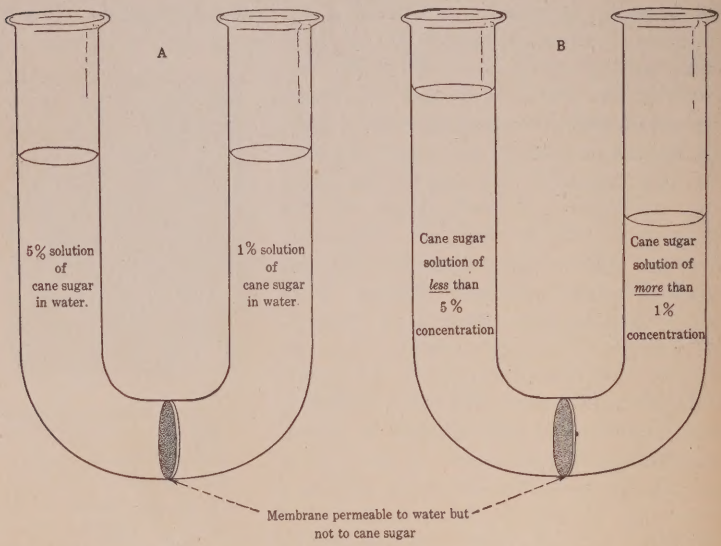

FIG. 69. — Diagram to show diffusion through a semipermeable membrane. A, at beginning of experiment; B, showing difference of level in the two solutions due to osmotic pressure at the close of the experiment. (From Holman and Robbins.)

The molecules of water may be pictured as passing through the interstices of the membrane until the ratio of the molecules of water to those of sugar is the same on both sides of the membrane. As the sugar molecules will not pass through these interstices, the water molecules must move from the weak solution towards the strong solution, thus increasing the volume of the latter and causing a pressure against its containing walls. This hydrostatic pressure causes the phenomenon known as **turgor**

[2] "The word 'osmosis' has been given such a variety of meanings by those who have used it that it has lost any precise meaning whatever" (Holman and Robbins).

in the plant cell. The pressure caused by the absorption of water distends the vacuole and presses the protoplasm against the plasma-membrane and this against the resistant cellulose cell wall.

When the solutions on either side of a semipermeable membrane are equal in molecular concentration, they are said to be **isotonic.** If they are unequal, the stronger solution is called **hypertonic** and the weaker solution **hypotonic.** If the cell is surrounded by a hypotonic solution, water enters the cell, causing turgor. If it is placed in a hypertonic solution, water leaves the cell, causing a collapse of the cell wall, a condition known as **plasmolysis.** The wilting of the leaf is due to the plasmolysis of its cells. In the animal cell, which has not the resistant cellulose wall, osmosis from a hypotonic solution may cause the actual bursting of the cell, known as **cytolysis,** while the wrinkling due to osmosis from the cell to a hypertonic solution is called **crenulation.**

Selective Permeability. — The plasma-membrane is permeable to water, oxygen, carbon dioxide, and ammonia. Of the various food components, it is most permeable to fats, less so to sugars and amino-acids. It is very little permeable to the inorganic salts. There is reason to believe that the plasma-membrane differs from the protoplasm internal to it in the higher concentration of the lipins at the surface. Possibly the reversal of phases between the lipins and other cell components in the plasma-membrane will serve to explain some of the phenomena known as selective permeability and one-way permeability. But in the present state of our knowledge, it is sufficient to call attention to the fact that the large number of metabolic reactions taking place within the cell affects the structure of its plasma-membrane. Then, to recur to our earlier analogy, the interstices of the membrane are constantly changing their size, shape, and number, and thus offering a changing resistance to the free diffusion of substances through the partition.

When the cell is injured or killed, the plasma-membrane breaks down in the sense that it becomes a permeable membrane, thus showing that its semipermeable nature is due to the metabolism of the cell alone.

THE CELL AND THE ORGANISM

The cell in its metabolism absorbs materials from the outside world through its plasma-membrane. Within the cell these are swept into the stream of metabolic reactions under the influence of intracellular enzymes. In this elaborate cycle of complicated

chemical activity, waste material accumulates and this is secreted through the plasma-membrane to the exterior. If in the course of metabolism the amount of protoplasm increases, the cell grows and may divide. In response to stimuli it may manifest changes in shape or activity. If it can perform all these activities independently of other cells it is said to be physiologically balanced.

Unicellular Organisms. — We have already spoken of protozoa and protophytes. These are individual cells or colonies of cells and often are assigned to the plant or animal kingdoms only with difficulty. For this reason they are sometimes grouped together as the **Protista.** One of the criteria used in separating the animal protists from the plants is the type of nutrition employed.

The green unicellular plants are equipped with chloroplasts and are therefore capable of photosynthesis. They utilize carbon dioxide and water and liberate oxygen. They are known therefore as **holophytic** in nutrition. Still other unicellular plants are colorless (yeasts, bacteria, etc.) and obtain the energy for their anabolic processes from other sources than sunlight (**chemosynthesis,** page 194). They absorb simple compounds from the medium in which they live and are characterized as **saprophytic.**

Most free-living unicellular animals ingest other and smaller organisms or parts of organisms and digest these in improvised food vacuoles. This is called **holozoic** nutrition. Some parasitic protozoa, on the other hand, utilize the digested foodstuffs of other and larger organisms, a phenomenon known as **saprozoic** nutrition. Many parasites, both plant and animal, take their food directly from the tissue of their host.

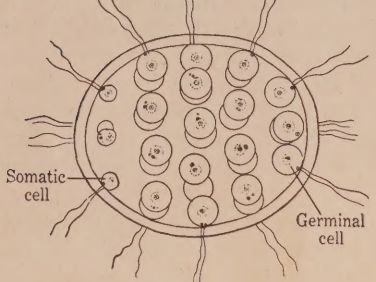

FIG. 70. — *Pleodorina illinoiensis*, a colonial flagellate, to show differentiation between germinal and somatic cells. ×250. (After Kofoid.)

Mixed types of nutrition are not unknown. The green flagellate protozoön *Euglena* can build up its food by photosynthesis, ingest bacteria, and absorb soluble compounds from its culture medium.

Among the colonial protozoa a division of labor is often observable. Thus in the colonial flagellate *Pleodorina* (Fig. 70), the larger cells are called **somatic**

as they can perform all the activities of the cell except those involved in sexual reproduction (Chapter VI), which is restricted to the smaller **germinal** cells. In the colonial protophyte *Volvox* (Fig. 71), the cells of the colony are connected by delicate protoplasmic connections, so that the contents of the individual cells have direct protoplasmic continuity.

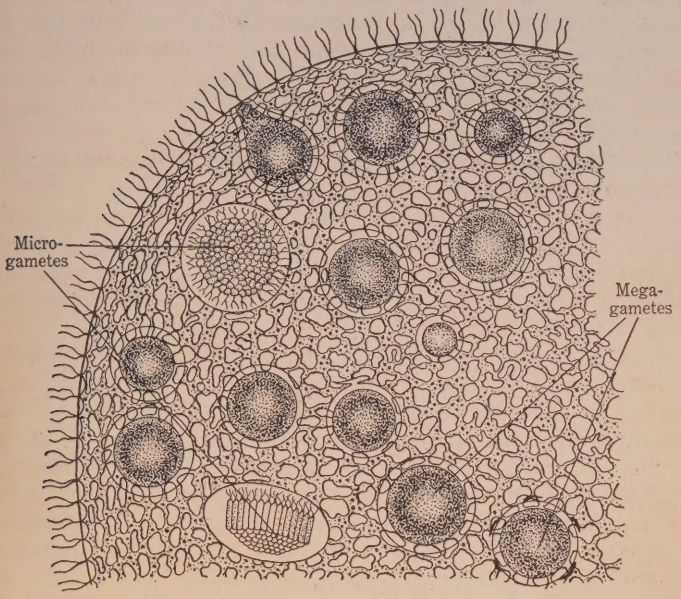

FIG. 71. — *Volvox globator*, a colonial flagellate, to show protoplasmic connections between the cells, and differentiation between microgametes (sperm) and megagametes (eggs). (After Cohn.)

Multicellular Organisms. — The cells of the multicellular organisms are called physiologically unbalanced as they are dependent upon each other for specialized functions. This phenomenon is called **differentiation** or division of labor. The majority of the cells are dependent upon a few (comparatively) for nutritive materials. In the frog, the cells lining the digestive system secrete the enzymes necessary for digestion and absorb the digested material, which are then circulated about the body. All animals have some sort of digestive surface, and if this itself does not insure an equitable distribution of the product, a cir-

culatory system of some sort will be found. In the plant, water is absorbed by the root hairs and conducted to the leaves where it is used in combination with atmospheric carbon dioxide for photosynthesis. In all plants so large that materials cannot diffuse easily from cell to cell, conducting tissues are present.

The tissues of all organisms resolve themselves into two principal classes, **lining** tissues and **connecting** tissues. In the plant, which has no internal cavities, the epidermis is the sole lining tissue. In the animal, where there are many cavities, we find such tissues lining the skin, the digestive tube, the body cavity, the blood vessels, all glands, etc. The nerves may be considered a highly modified lining tissue.

Connective tissue in the plant consists of parenchyma, relatively undifferentiated, the fibro-vascular bundles with the function of support and conduction, etc. In the animal we distinguish connective tissue, cartilage, and bone. Blood may be considered a specialized connective tissue with a fluid matrix, and muscle cells likewise are highly specialized connective tissue cells with contractile fibers.

We may think of the multicellular organism as a whole composed of many individual cells aggregated in tissues with particular characteristics. In the more highly organized forms the different types of tissues are combined in organs with particular functions. All the organs whose functions are concerned with some particular activity of the organism as a whole make up an organ system. The wheat plant has relatively few organs, root, stem, leaf, and flower. The frog has many organs arranged in ten organ systems, digestive, respiratory, circulatory, excretory, endocrine, skeletal, muscular, nervous, sensory, and reproductive. As we have seen, the activities of these organ systems of the animal are closely interrelated and tied together by that common carrier, the blood, the circulating endocrines, and the coördinating nervous system, by means of which the activities of all the cells are united in the activities of the organism as a whole.

The existence of intercellular connections in both plant and animal tissues has been used to deny the validity of the cell theory as applied to multicellular organisms. For example, it has been said that these are masses of protoplasm partially separated by cell-membranes. Similarly it has been held by some that the protista are not unicellular but acellular organisms. The arguments, however, have not met a ready acceptance, and the ma-

jority of biologists will agree with the conclusion of Wilson that the multicellular body is an aggregate of cells so differentiated and integrated that they form what he terms a "cell-state."

The organism from the point of view of its metabolism may be compared with that economic organization, a vertical trust, which controls the production of many different raw materials, the manufacture from these of refined basic commodities, elaborate transportation systems, factories where innumerable trade articles are manufactured, storage warehouses, and distributing chain stores. Yet such an organization, great and complex though it is, acts as a unit in the financial world to show an annual profit or a loss. So the most highly organized plant or animal acts as a whole even though it is composed of organs, tissues, and cells.

CHAPTER V

THE CELL AND BEHAVIOR

By the **behavior** of an organism is meant its activities in relation to its surroundings or environment. In the analysis of metabolism, or the transformations of matter which take place within the body of the organism, it was seen that these were accompanied by transformations of energy. Thus it is possible to classify the chemical reactions which are involved in cellular metabolism as endothermic or exothermic according to whether energy is stored or liberated. A large part of the energy liberated in exothermic reactions is immediately utilized in simultaneous endothermic reactions, so that there is a certain equilibrium of energy within the cell.

But just as there is an interchange of material between the cell and its environment in absorption and secretion, so there are accompanying transformations of energy, continuous and proportionate to the metabolic exchange. Thus the photosynthetic cells of the green plant convert the radiant energy of sunlight into potential chemical energy, which the animal cell in turn releases in the processes of digestion and dissimilation.

IRRITABILITY OF THE CELL

We shall not attempt to discuss these regular or continuous energy transformations which parallel the chemical reactions of cellular metabolism. In the behavior of the organism we are concerned particularly with those transformations of energy which appear in response to relatively slight but sudden changes in the equilibrium of the environment which are called **stimuli.** Responses of this type are explosive in their speed and completeness and are not proportionate to the amount of stimulation.

The responses of the organism, like its metabolic activities, can be reduced to cellular phenomena. During the ordinary or continuous transformations of energy which accompany the metabolism of the cell, the equilibrium of forces within the cell is practically undisturbed. But when a change in the equilibrium of the environment acts as a stimulus, the cell responds by the

sudden transformation of potential into kinetic energy, accompanied of course by chemical reactions. This ability of the cell to respond in such a manner is known as **irritability.**

The Stimulus. — Changes in the equilibrium of forces outside the cell, the environment, act as stimuli and are therefore classified according to the form of energy which is affected. Thus we distinguish **mechanical** stimuli due to changes of impact, touch, pressure (including that due to osmosis), and sound waves. **Chemical** stimuli are the result of changes in the composition and concentration of chemical substances. **Electrical** stimuli are due to changes in the direction, wave length, and strength of electric currents. **Photic** stimuli are the result of changes in radiant energy of light, such as changes in its intensity, direction, and wave length. **Thermal** stimuli are simply changes in temperature.

The Response. — The cell responds to stimulation by releasing energy in one or another of its many forms. So there are mechanical responses expressed by the movement of the cell or some of its parts, changes of shape, etc. Chemical responses are seen in sudden changes of concentration and composition. Secretion as an explosive response appears to be a combination of these two. Electric discharges are a form of response manifested by some fish, such as the electric ray, and there is ground for belief that all cells respond to stimulation by the production of a short and weak electric current which may stimulate neighboring cells to a similar response. This so-called **bioelectric current** is of great importance in the theory of the nervous discharge to be considered in a later section of this chapter. Photic response is by the production of light by such animals as fireflies and by many marine organisms which are responsible for the so-called phosphorescence of the sea. Thermal response, i.e., the production of heat, is seldom if ever a direct response to stimulation but is a concomitant of chemical response, as in the fever developing after an infection. The production of heat also accompanies other forms of response, especially muscular activity.

Excitation and Inhibition. — A closer analysis of the behavior of the cell following the application of a stimulus indicates two periods: (1) a period of **excitation,** in which the cell responds to the stimulus, and (2) a period of **inhibition** (period of **relaxation** in muscle, **refractory** period in nerve) during which the cell will not respond to the stimulus. The period of inhibition is the time

during which the cell is reorganizing after the sudden output of energy. It is during the second period that the consumption of oxygen and liberation of carbon dioxide characteristic of stimulated cells take place. This increased respiration is symptomatic of oxidative reactions which supply the energy for the reorganization of the cell.

BEHAVIOR OF UNICELLULAR ORGANISMS

Independent cells as represented by unicellular organisms respond to stimulation by movement towards or away from the source of the stimulus (positive or negative **tropisms**). The amoeboid movement characteristic of many protozoa, the white blood corpuscles, and other independent or semi-independent cells, as it has been studied in *Amoeba* (Fig. 72), consists of the protrusion of finger-like processes in the direction of movement and the gradual flowing of the remaining protoplasm into one or more of these **pseudopodia.** A recent explanation of this phenomenon has been offered in terms of phase-reversal (Fig. 73).

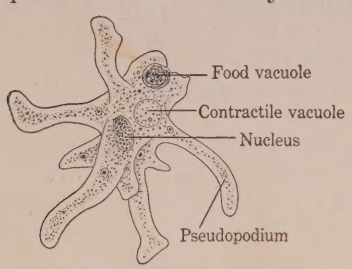

FIG. 72. — *Amoeba proteus,* to show pseudopodia. (After Doflein.)

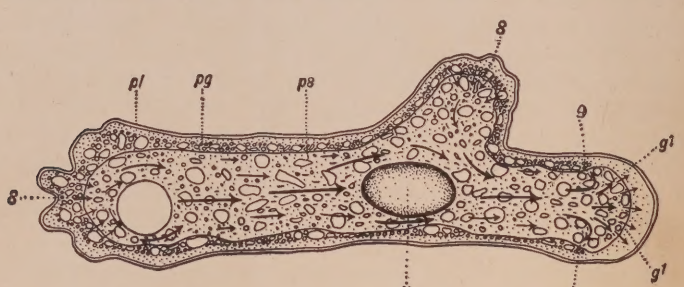

FIG. 73. — Diagram to illustrate Mast's theory of pseudopodial locomotion in *Amoeba. pl,* plasma-membrane; *pg,* gel; *ps,* sol; *g* and g^1, regions of gelation; *s,* region of solution; *N,* nucleus. (From Curtis and Guthrie.)

The protoplasm within the plasma-membrane consists of an external gel and an internal sol. In forward locomotion contractions

of the cell push the sol forward where it is converted into gel, while the gel in the posterior portion of the cell reverts to the sol condition preparatory to flowing forward. No cell organelles for the reception of stimuli, or for locomotion, can be distinguished.

In other protozoa and protophyta, such organelles for reception, locomotion, and coördination are well known. The flagellates, for example *Euglena* (Fig. 64), move by the lashing of one or more whip-like flagella. These frequently have basal bodies

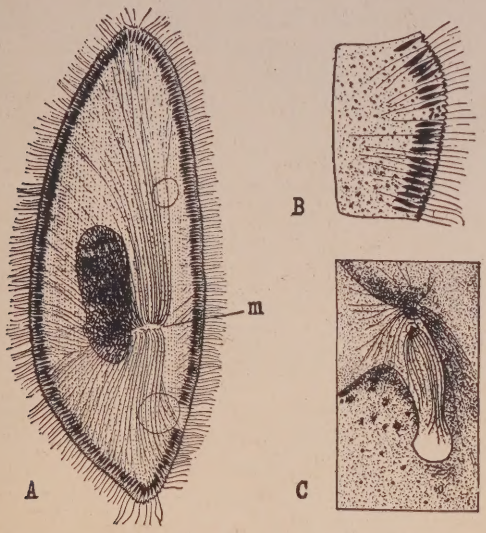

FIG. 74. — *Paramecium caudatum*, neuromotor mechanism. A, fibers radiating from motorium (m); B, fibers attached to cilia and trichocysts; C, centers in region of gullet. (After Rees, from Curtis and Guthrie.)

connected with the centrosome by a delicate filament. The flagella may act as receptors for most types of stimuli, as they frequently are at the anterior end of the cell. *Euglena* and many holophytic unicellulars have red pigment spots which are thought to act as photoreceptors. Ciliated cells like *Paramecium* (Fig. 67) move by the oar-like action of many tiny vibratile hairs called **cilia**. These cilia may also act as receptors, and are connected with each other and with the **trichocysts** (tiny bodies discharged as threads apparently as a " defensive " response) by a complex system of fibers called the neuro-motor system (Fig. 74). The

behavior of *Paramecium* in response to stimulation of various types has been studied, particularly by Jennings, who finds that its reactions are of the trial-and-error variety. Thus when *Paramecium* encounters an obstacle, either solid or chemical, it reverses the action of its cilia and backs away (thigmotropism or chemotropism). Then swimming forward again with a slight change of direction, it may strike the obstacle once more, in which case the backing and filling is repeated. This continues until at length the obstacle is cleared.

Tropisms. — Changes in the direction of position, growth, or locomotion determined by the source of stimulation such as those referred to above are known as tropisms. They are classified according to the type of stimulus, as thigmotropism (mechanical), galvanotropism (electrical), chemotropism (chemical), phototropism (photic), etc. Special tropisms already mentioned (Chapter III) are geotropism, with reference to gravity, and hygrotropism with reference to water, etc. Some authors restrict the use of the word tropism to changes in the direction of growth and use the suffix **-taxy** or **-taxis** for changes in the direction of locomotion.

BEHAVIOR OF MULTICELLULAR PLANTS

In the multicellular plants response to stimuli is seldom a sudden explosive affair. Sensitivity to stimuli is manifested primarily by the slow changes of the direction of growth known as tropisms. While no special receptor organs are developed, the growing tips of the root and its branches, and of the shoot and its branches, are more sensitive than the other regions. It is evident from the experiments on seedlings cited on page 64 that the excitation is conducted in some way to the region behind the growing tip, for here the response is made by a curvature of root or shoot. The curvature appears to be due to a decrease in the turgor of the cells on the side towards which the tip bends, in other words to the osmosis of water from those cells. This is followed by the deposition of cellulose, which stiffens the cells in the new position, corresponding to the period of reorganization.

In some few plants special organs for reception are known to exist, particularly in the insect-eating forms such as the Venus flytrap, *Dionaea* (Fig. 75). Here the leaf is equipped with three hairs in the center of the upper surface which are thigmoreceptors (sensitive to touch). When an insect lights on the leaf, attracted

FIG. 75. — *Dionaea muscipula* (Venus' flytrap). The leaf at the left has closed and entrapped an insect. (After Payne, from Holman and Robbins.)

by the secretions of glandular hairs on the surface, and touches the sensory hairs, the two halves of the leaf fold up quickly along the midrib, trapping the insect by means of the stout teeth of the upper margin. The secretions of the glandular hairs referred to contain enzymes by means of which the soft parts of the insect are digested. In this case the receptors are the sensory hairs, transmission is probably through the sieve tubes of the veinlets, and the effectors are the cells along the midrib, which cause the movement by their loss of turgor, and the secretory cells of the gland-hairs.

BEHAVIOR OF MULTICELLULAR ANIMALS

In the less highly organized multicellular animals such as *Hydra* (Fig. 76), a relatively simple sensory-neuro-muscular complex is found. This organism has but two tissues, an external layer called the ectoderm, and an internal layer called the endoderm, with an intercellular matrix, the **mesogloea,** between the two (Fig. 77). The bases of the ectodermal cells project into the mesogloea and extend at right angles to the long axis of the Hydra. Those of the endodermal cells also are embedded in the mesogloea but extend in the direction of the long axis. These bases contain contractile fibers (**myofibrils**) extending the length of the base, which is therefore known as a muscular process. These cells can respond directly to stimulation, being both receptor and effector, and since they transmit the excitation from one to another, they may be said to combine all the factors of the complex in themselves (cell-to-cell transmission). There are also specialized sensory cells found in both layers, those of the endoderm being equipped with sensory flagella. The basal ends of these receptor cells form branches which communicate with each other, with the muscular bases of other cells, and with the specialized nerve cells. A sensory cell and a cell furnished with a muscular base form a two-cell sensory-

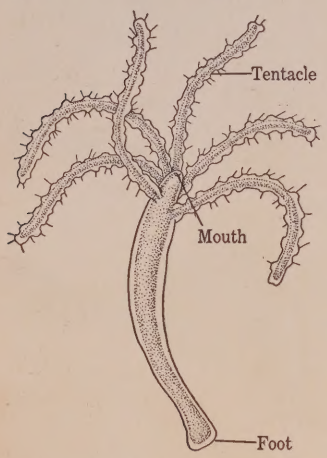

FIG. 76. — *Hydra viridis* (green Hydra). The digestive cavity (coelenteron) is indicated by stippling. ×10.

neuro-muscular complex. Finally there are specialized nerve cells, with long, slender branches which come in contact with

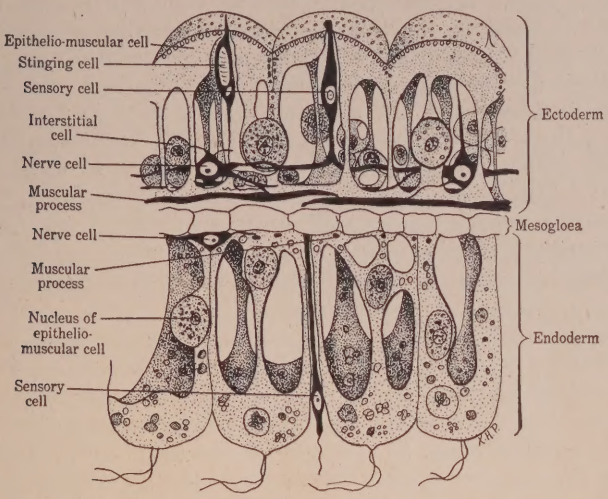

FIG. 77. — *Hydra viridis*, a diagram of the cell structure, highly magnified. (After Hadzi.)

those of other cells, such as the sensory cells, and those with muscular bases. They form a network of fibers called the **nerve net** by means of which the excitation stimulated in sensory cells is transmitted to bring about a more rapid contraction of many muscular processes than would follow the slower transmission through the muscular processes themselves.

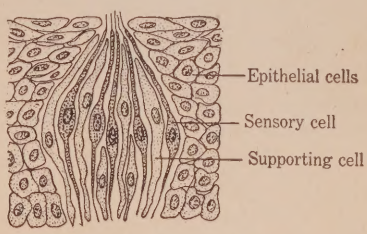

FIG. 78. — Diagram of human taste-bud to show flagellate sensory cells. (After Curtis and Guthrie.)

Many types of epithelial cells in multicellular animals are ciliated or flagellated. These, as on the tongue, or lining the oesophagus, of the frog may serve to pass food down the alimentary canal. Those found in the epidermis of the early tadpole stages are the first locomotor organs to develop. Often the cilia or flagella are entirely sensory, as in the case of receptor

organs, e.g., the taste buds (Fig. 78). The behavior of such ciliated or flagellated cells in the higher animals appears to depend upon the direct transmission of stimuli from cell to cell, as no particular apparatus for such transmission has been described.

Cell-to-cell transmission, or even nerve-net transmission, however, plays a relatively small part in the behavior of the highly organized vertebrates. As we have already seen in the case of the frog these have a complicated and highly irritable sensory-neuro-muscular (or glandular) complex by means of which they respond to the varied stimuli to which they are exposed. This apparatus comprises (1) specialized receptors which are excited by different types of stimuli, (2) conductors which transmit the excitation through a nervous discharge to (3) the effectors, contractile muscles, or secretory glands.

Receptors. — The receptor of vertebrate animals is a cell, the structure and metabolism of which are specialized, in the sense that only a particular type of stimulus will cause excitation. Thus the cells of the retina are excited by light waves alone, the cells of the **spiral organ** (of Corti) in the cochlea of the ear respond only to vibrations of specific wave lengths in the endolymph, and the flagellate cells of the taste buds respond to particular chemical compounds.

The sense organs are composed of many tissues with covering, supporting, and circulatory functions, but the only receptors are modified epithelial cells such as those mentioned above. In a few cases, the olfactory receptors, for example, the sensory (afferent) neurone itself is the actual receptor and transmitter, like the sensory cell of the hydra. In a few others the axon of the sensory neurone appears to be a receptor (free nerve ending) but it is more probable that this is a transmitter only of the excitation aroused in neighboring unspecialized epithelial cells.

The olfactory, gustatory, auditory, and the equilibratory receptors (in the semicircular canals of the ear) are all flagellated cells. Nothing is known regarding the metabolic changes produced in them by stimulation, other than the general theory that these are exothermic in nature. The nature of the changes in the retinal cells (rods and cones) produced by the stimulation of light waves is in dispute, but the presence of a substance known as visual purple is undoubtedly concerned in the process.

Conductors. — The state of excitation induced in a receptor by a stimulus, acts itself as a stimulus to induce a state of excitation in a sensory or afferent neurone. Commencing at the

distal end, that is to say the end farthest from the central nervous system, this state of excitation is transmitted along the axon to the synaptic junction with an intermediate or a motor (efferent) neurone. We shall hereafter speak of the transmitted state of excitation as the nervous impulse. Although the receptors are specific so far as the type of stimulus by which they are excited is concerned, this is not true of the neurone. Any type of stimulus will result in the transmission and discharge of a nervous impulse. Thus while the rods and cones are sensitive to light waves only, pressure on the eyeball transmitted to the optic nerve will produce visual sensations. This is true also of the motor neurones. The gastrocnemius muscle of the frog contracts whenever the sciatic nerve is excited by mechanical, chemical, electrical, or even thermal stimuli. The transmission of a nervous impulse is accompanied by an electric current, and some authorities consider that this action current is the mechanism by which the impulse is transmitted. The greatest speed of transmission is 120 meters per second (motor nerves of mammals), much less than the rate of transmission of an electrical current through wire or air. It is also held that the impulse is due to metabolic changes in the axon induced by the bioelectric current.

Even among the vertebrates there are other methods of transmission than the nervous impulse. The ciliated cells of the mouth and throat of the frog continue the wave-like beat of the cilia extending from cell to cell, even after they are removed from the body. The muscle fibers of that great muscle, the heart, transmit a state of excitation one to another. The neurone type of transmission, however, is the primary method of obtaining responses to stimuli.

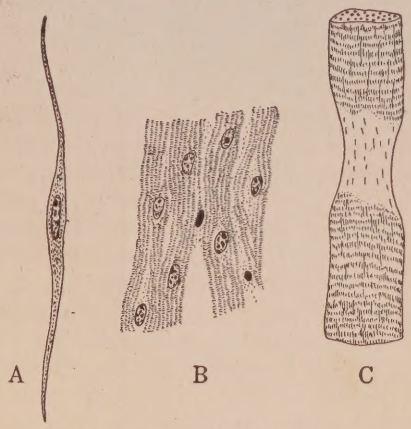

Fig. 79. — Human muscle cells. A, smooth muscle fiber; B, heart muscle; C, striate muscle fiber. (After Hill.)

Effectors. — The principal effectors of the vertebrate body are the muscles. The muscle cells, striate or non-striate (Fig. 79),

are characterized by the presence of myofibrils, delicate threads which, by their shortening, effect the contraction of the cell. These may be compared with the contractile fibers found in some protozoa, such as the stalk of *Carchesium* (Fig. 80). The striate muscle fibers are not single cells but multinuclear syncytia in which the parallel rows of myofibrils show regions of alternate thickness and thinness. This produces the effect of stripes alternately light and dark, on account of which the muscle receives its name. The heart muscle is intermediate in position between striate and smooth muscle in that its fibers are single cells, striated, and united by protoplasmic processes so that excitation can be transmitted directly from cell to cell. This seems comparable to the method of transmitting impulses between the musculo-epithelial cells in *Hydra*.

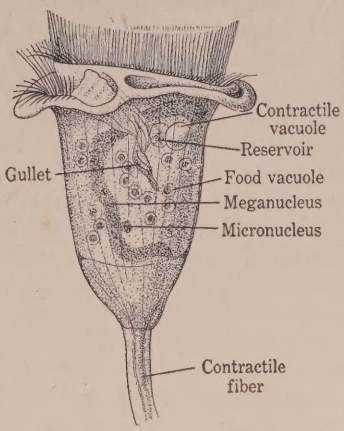

FIG. 80. — *Carchesium polypinum*, a ciliate protozoön. The vibrating tongue which hangs down in the gullet is formed by the fusion of long cilia. (After Doflein.)

Striate Muscles. — The striate muscle fibers are excited only by the discharge of a nervous impulse through the myoneural junction (Fig. 81), and each fiber is supplied by a separate motor neurone. The smooth muscle cells, however, still retain the ability to transmit impulses from one to another, while the anastomosing processes of the cardiac muscle result in the extremely rapid transmission of impulses through the entire organ.

The contraction of the muscles is due to the conversion of glycogen to lactic acid, with the liberation of a small amount of chemical energy. The acid acts on the myofibrils by causing them to contract, as any strong acid will result in the contraction of proteins. This can be demonstrated by the action of acids on albumen. After this contraction period about one-fifth of the lactic acid is oxidized to give enough energy for the formation of glycogen again from the remaining four-fifths. During the process a considerable amount of energy is dissipated as heat, and the end-products of carbohydrate metabolism, water and carbon dioxide, are formed, in appreciable amounts. The period

of contraction includes a latent period (0.01 sec.) and a contraction period (0.04 sec.). The period of reorganization includes a relaxation period (0.05 sec.) and a period of recovery in which the glycogen is resynthesized. Repeated stimulation at intervals shorter than the normal period of recovery results in the continued contraction of the muscle (tetanus) followed by the inability of the fiber to contract (fatigue).

Smooth Muscles. — The smooth muscles, however, are able to maintain a continued state of contraction over long periods after an initial stimulation. They respond directly, by contraction, to at least one stimulus, that of being stretched. The result of two antagonistic sets of smooth muscle fibers is that of an alternate stretching and contracting, transmitted independently of the central nervous system, and so causing the slow wavelike involuntary activities characteristic of some visceral muscles.

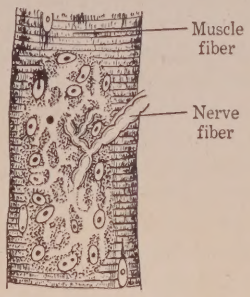

FIG. 81. — A diagram to show the myoneural junction at which a nervous impulse is transmitted from a nerve fiber to a muscle fiber. (After Curtis and Guthrie.)

Glands as Effectors. — The explosive discharge of substances through the plasma-membrane of gland cells may be considered as an effector response to a nervous impulse. These gland cells are specially modified epithelial cells, which manufacture and discharge particular substances, such as mucus, digestive enzymes, and wax. Many cells discharge their contents continuously, but some do so only as an explosive response. These are usually aggregated into organs called glands which are provided with ducts, e.g., liver, pancreas, etc., but in other cases secrete their products directly into the blood stream, e.g., thyreoid, adrenal, etc.

The glandular response is due to the nervous impulse transmitted by a motor neurone, and like the muscular response involves two phases, the period of discharge, corresponding to the active period of all specially irritable cells, and the period of reorganization which we have recognized in sense cell, nerve cell, and muscle cell.

The period of discharge is comparable with the tropic response of the plant cell, in that changes of osmotic pressure are involved. A current of water, probably drawn from the intercellular lymph

spaces, is swept across the gland cell, accumulating the stored products, and carrying them through the plasma-membrane, which seems to have an increased permeability at this time.

The period of recovery is occupied by the gland cell in the preparation of the particular substances with regard to which it is specialized.

Metabolic Coördination. — There is an intimate connection between the internally secreting or endocrine glands and the sensory-neuro-motor complex, owing to the effect of the former on the metabolism of the organism or of its several parts. This connection is frequently referred to as chemical coördination, but in accordance with the more or less arbitrary distinction adopted in this text, the term **metabolic coördination** is used in order to distinguish it from the irritable coördination of the sensory-neuro-motor complex.

Adrenalin. — An extreme example of this interrelationship is seen in the action of adrenalin, an endocrine secreted by the adrenal gland (page 21). This substance circulating in the blood affects the smooth muscles innervated by the motor neurones of the autonomic system in the same way as a nervous impulse from these neurones themselves. Thus the beat of the heart may be accelerated, the peripheral blood vessels constricted, hair erected, etc. The embryological development of the adrenal gland shows that the cells which secrete the adrenalin are modified autonomic ganglion cells, that is to say, motor neurones. Like the autonomic ganglia they have synaptic connections with motor neurones of the spinal nerves by way of the communicating branches. There are, then, two routes by which these smooth muscles are excited: first, by way of the autonomic neurones, and second, by way of the increased adrenalin circulated in the blood. This double action is important in the consideration of animal behavior.

The Reflex. — The response of the cell to a change in the environment is due to its irritability, or property of energy transformation, and involves the three activities of receiving stimuli, transmitting the excitation, and effecting a response. Special types of cells are developed in the multicellular animals for each of these functions, the whole forming a sensory-neuro-motor complex. The response effected directly through this mechanism to a single stimulus is called a **reflex,** because of the analogy to the reflection of light waves. The simplest type of mechanism involved is the reaction of a single cell like an epithelial cell of

Hydra. The next involves the action of at least two cells such as a sensory and an epithelial cell in the same animal. Then there is a three-cell combination, e.g., sensory cell, nerve cell, and epithelial cell, also found in *Hydra.* But the combination to which the word reflex is generally applied involves the series of four cells, receptor, sensory neurone, motor neurone, and effector, known as the simple reflex arc of the vertebrate. Such reflexes with a single synaptic junction are considered the units in the pattern of animal behavior.

The Nervous Impulse. — The direction of the nervous impulse is always from the axon of the sensory to the dendrites of the motor neurone. Experiments indicate that there is normally an exceedingly small but still demonstrable delay in the transmission of a nervous impulse across the synapse, which can be prolonged or shortened by external factors such as drugs, or by internal factors, namely, the number, frequency, and duration of previous stimuli.

The Synapse. — As we have seen, through the intervention of intermediate neurones, every sensory neurone is potentially in communication with every motor neurone in the body. Only potentially, however, as otherwise every stimulus would excite every effector in the body, just as every stimulus transmitted to the nerve net spreads across it in every direction practically simultaneously. The nerve net is like an exaggerated party line in which the telephone bell rings at the instrument of each subscriber. In the synaptic system we might say, to continue the analogy, the bell will not ring unless the receiver is on the hook, at that particular instrument.

The Recovery. — Following the discharge of a nervous impulse the period of recovery includes three stages, known as (1) the **refractory** period in which no impulse can be transmitted, (2) the **subnormal** period in which only stimuli stronger than usual will cause excitation, and (3) the **supernormal** period in which stimuli weaker than usual will excite the nerve. If the frequency of stimulation is timed so as to fall in successive subnormal periods the synaptic delay will be prolonged and the particular synapse will be cut out of the system, thereby inhibiting a particular reflex. If the frequency of stimulation is such as to bring successive stimuli in successive supernormal periods, stimuli too weak in themselves to transmit an impulse across the synapse may effect a summation of stimuli which will produce that effect, and bring about a reflex.

Relaying the Impulse. — There are few such simple two-neurone reflexes. The existence of the intermediate neurones found in such numbers in the spinal cord and brain and their synapses with sensory, motor, and other intermediate neurones indicates the existence of the most complicated and involved routing of impulses throughout the system. What determines these paths?

The Route. — A suggestive hypothesis is that the impulse follows the path of least resistance. Coming towards the central nervous system over a special sensory neurone, the impulse is discharged across the synapse or synapses offering the least delay. It is then transmitted along one or more intermediate neurones or relays of neurones, again being discharged across those synapses which offer the least delay. These finally transmit the impulse across the most rapidly yielding synapses to the motor neurones which awake the response of the effectors.

Consider then the number of sensory impulses continuously converging towards the central nervous system. From more than twenty types of exteroceptors, not to mention the innumerable proprioceptors of the viscera, muscles, joints, and tendons, nervous impulses are traversing the synaptic net. Granted that each would evoke an appropriate reflex by itself, it is evident that some reflexes would be antagonistic to others, just as some would supplement the effect of others. How are these sensory impulses coördinated?

In the first place we may suppose that every impulse in addition to following the paths of least resistance open to itself, increases or decreases the synaptic delay of every synapse which it passes, whether or not it crosses the synapse itself. This affects directly the routing of succeeding impulses. The opening of a new synaptic route, so to speak, makes the subsequent passage of an impulse along that route more rapid. The greater the number of intermediate neurones concerned, the more complex and unpredictable will be the response to an initial stimulus. The pattern and order of the reflexes will vary according to the possible routes of the impulses, their number, strength, and duration.

Chain Reflexes. — The simple reflex evokes a simple response. But in some cases an initial stimulus arouses a series of effectors, and a more complicated response. These are known as **chain reflexes** and often they involve the simultaneous or successive contraction of many muscles in different parts of the body. Some reflexes, particularly the more complex chain responses,

are sometimes known as **instincts.** The use of this word carries with it the connotation that the pattern and order of the reflexes are inherited, and that is one of the hotly debated points in the study of animal behavior today.

Modified Reflexes. — Simple and chain reflexes are modified by repetition of the same type of stimulus, apparently because of changes in the length of the synaptic delays involved. They are modified, for the same reason, by the effect of other types of stimuli occurring simultaneously. They are also modified by repeated association with other reflexes.

Conditioned Reflexes. — This last type of modification produces what is known as the **conditioned reflex.** Pavlov, the Russian scientist who initiated this line of investigation, based his work on the simple reflex, salivation in dogs. The sight of food causes the secretion of the salivary glands. When the ringing of a bell accompanied the presentation of the meat, an association was made between the two stimuli. Later, after a number of repetitions of the double stimulation, it was found that the ringing of the bell alone would produce stimulation so that the associated stimulus could be substituted for the original one, although it produced no effect on dogs which had not been conditioned.

Association. — More complex conditioned reflexes have since been studied, but the basis of all these lies in new associations between stimuli and reflexes, and these in turn in the opening up of new synaptic connections between sensory neurones. These occur by the intervention of intermediate neurones in the cerebral cortex, which is therefore the seat of association and the highest center of the synaptic net. Psychologists have localized different areas of association in the cortex of the cerebrum, which in man is a sheet containing nearly ten billion intermediate neurones. The synaptic connections possible are beyond the powers of calculation and will account for all the infinite variety of even human behavior.

Learning. — The conditioning of reflexes, or the establishment of new associations based on the substitution of stimuli, through the intervention of new cerebral synapses, is what we call learning and habit formation that is to say, acquired behavior.

Memory. — By learning, the student of animal behavior means conditioning, or formation of new associations and substitutions of stimuli. By habit formation he understands the establishment of a new reflex arc, through the continued discharge of

nervous impulses across the synapses involved. Memory, then, in terms of the synapse, involves the renewed use of a reflex arc after a period of disuse. The loss of memory, so called, is the result of a disturbance in a particular synapse (blocking), thus cutting out one or more intermediate neurones and causing a detour, or in more aggravated cases, the temporary or permanent injury to some region of the brain.

Intelligence. — Intelligence, as the word is used by students of animal behavior, means the capacity for learning or conditioning. This, we have seen, depends on the development of the cerebral cortex in vertebrates. In the lower vertebrates, fish and amphibia, this capacity is very slight, and the cortex is hardly developed. In reptiles and more particularly among the birds and mammals, where a cerebral cortex is more highly developed, a greater power of association exists. In man, the cerebral cortex is most highly developed, and forms the largest part of the brain. Most sensory impulses are eventually routed to this region (sensory areas), and after circuitous routes among the neurones of the association area are discharged from the neurones of the motor areas whose long axons stretch to all parts of the brain and cord.

Visceral Behavior. — The types of behavior mentioned above concern the skeletal muscles primarily, as the visceral muscles are excited primarily through the autonomic nervous system. The action of these visceral muscles often results in phenomena which the psychologist calls emotional behavior. The bristling of the hair, elevated by smooth muscles in the skin; the perspiration caused by the explosive discharge of the sudoriparous glands of the skin; the dilation or constriction of the blood vessels; the acceleration or deceleration of the heart beat; and many other so-called involuntary actions, are symptomatic of relatively rapid response on the part of the visceral musculature. Responses of this type are due to the discharge and circulation of endocrines such as adrenalin which control metabolic coördination.

The discharge of adrenalin, however, is referred to the central control of the nervous system, from which efferent neurones carry impulses to the adrenal gland. The general route, then, without attempting to trace the individual neurone arcs, is:

receptor → sensory neurone → intermediate neurones → motor neurone to autonomic ganglion → motor neurone from autonomic ganglion to adrenal gland → discharge of adrenalin → circulation of adrenalin → contraction of smooth muscles.

Neurological Basis of Behavior. — It will be seen that in many cases the origin and routing of the nervous impulse, which results

FIG. 82. — *Amblystoma punctatum*, the salamander. $\times\frac{2}{3}$. (From Coghill, "Anatomy and the Problem of Behavior," by permission of The Macmillan Co., publishers.)

in some complex or delayed response, must necessarily be obscure. But the metabolic activities of the organism are ascribed to the chemical reactions of protoplasm, even though the formulae of the compounds and the equations of the reactions have not yet been established. With equal reason we can ascribe the complex phenomena of animal behavior to the pattern and order of the reflexes, to the synaptic network, to irritability, and the energy-transformations of which the cell is capable because of its complex metabolism.

Development of Behavior. — The development of the reflex has been studied by Herrick and Coghill in the case of the tailed amphibian *Amblystoma punctatum* (Fig. 82). The earliest form of locomotion involving the use of muscles developed by the early larva of this form is the swimming reflex. In its development five physiological stages can be demonstrated as follows: (1) a non-motile stage in which the muscles can be made to contract by direct stimulation, e.g., by the use of a sharp needle, but do not respond to a light

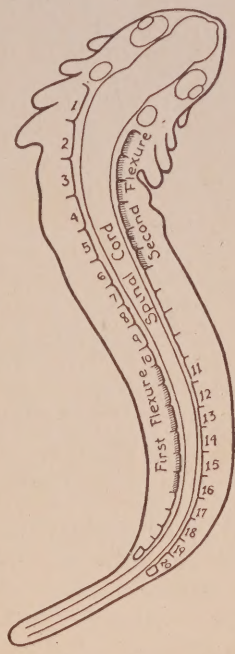

FIG. 83. — Diagram to show the swimming movement of an *Amblystoma* larva. Note that the first flexure has passed tailward, while a second flexure is beginning at the anterior end. The contracted muscle segments are indicated by cross-hatching. (From Coghill, "Anatomy and the Problem of Behavior," by permission of The Macmillan Co., publishers.)

touch on the skin; (2) an early flexure stage in which the embryo bends away from the side touched; (3) a coil stage in which the embryo continues the flexure until it twists itself into a tight coil; (4) an "S" stage in which before the coil is complete a second flexure in the opposite direction is commenced, so bending the embryo in a figure like the letter "S" (Fig. 83); and (5) the repetition of this action with sufficient strength and continuity to propel the animal forward.

Neurological Stages. — Corresponding developments take place in the nervous system. In the non-motile stage the spinal cord

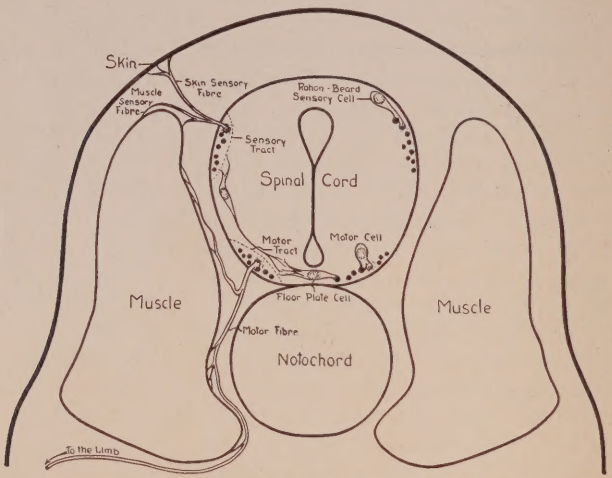

FIG. 84. — Diagram of cross-section through dorsal region of larva to show spinal cord, muscle segment, and skin, with the sensory and motor neurones. Note particularly the floor plate cell, and the intermediate neurone leading from sensory tract to floor plate cell. (From Coghill, "Anatomy and the Problem of Behavior," by permission of The Macmillan Co., publishers.)

(Fig. 84) contains both sensory or afferent neurones and motor or efferent neurones, the latter supplying the first twelve myotomes or muscle masses. The former (Rohon-Beard sensory cells) in the dorsal part of the cord send fibers to the skin (exteroceptive) and to the dorsal ends of the myotomes (proprioceptive). The bodies of the neurones in the cord itself form sensory tracts conducting headward. The motor neurones send fibers to the central portions of the myotomes and in some cases send branches passing beyond the myotomes to the developing forelimb. The bodies

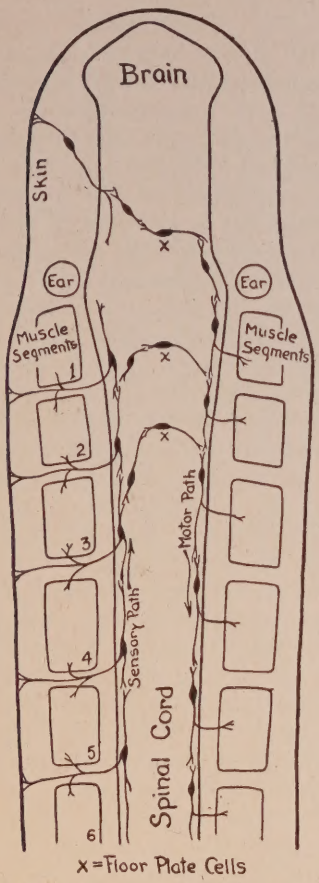

FIG. 85. — Diagram to show the neurone mechanism involved in the initiation of a single flexure away from the side stimulated. A stimulus applied to the skin, in front of or behind the ear, or directly to a muscle segment, excites a sensory neurone (shown on the left). The sensory path leads to the brain or anterior part of the spinal cord, where the impulse is transmitted by an intermediate neurone and a floor plate cell (x) to the motor path on the opposite side (on the right of the diagram). This path leads tailward so that the muscles contract in order from head to tail. This produces a coil away from the source of stimulation. (From Coghill, "Anatomy and the Problem of Behavior," by permission of The Macmillan Co., publishers.)

of these neurones in the cord form motor tracts conducting tailward. A third type of neurone, the floor plate cell, is an intermediate neurone of the commissural (transverse) type but does not establish synapses as yet with the others.

When the flexure stage appears, however, still another type of intermediate neurone (Figs. 84, 85) establishes synaptic relations with the sensory tract on one hand and a floor plate cell on the other. Thus a stimulus to the skin on one side is conducted via (1) a skin sensory fiber to the sensory tract, thence to (2) an intermediate neurone, and so to (3) a motor neurone on the opposite side. This causes the immediate contraction of the muscle segment innervated by the motor neurone, and as the nervous discharge passes down the motor tract, brings about the contraction of the posterior myotomes one after another. In this way the embryo bends away from the source of stimulation.

The development of these synaptic connections in the posterior segments accompanies the appearance of the coil stage.

The "S" stage is characterized by the appearance of collateral branches of the motor neurones which also establish synaptic relations with the floor plate cells in the anterior part of the spinal cord (Fig. 86). It is suggested that the nervous impulse transmitted by these collateral branches to the motor tract of the opposite (e.g., right) side may originally act as an inhibitor to the contraction of the myotomes on the right side and thus facilitate the contraction of those on the left, instead of opposing them. Subsequently a proprioceptive impulse would be initiated in the sensory tract from the contracted myotomes, and this, conducted across the intermediate neurones and floor plate cells, would excite the myotomes on the right which were formerly inhibited. This stimulation would bring about the contraction of the myotomes on the right, while inhibitory discharges conducted along the collateral branches to the motor tract of the left side would terminate the contraction of the corresponding myotomes. In this way a second flexure in the reverse direction would be started at the anterior end, while the first flexure was still progressing towards the posterior end.

The continued use of these reflex arcs brings about the fifth stage or that of locomotion.

In a similar manner the development of the limb movements, walking, the gill movements, and the movements of the mouth in feeding proceed with the same parallelism between the neurological phenomena and the pattern of behavior. At each stage of

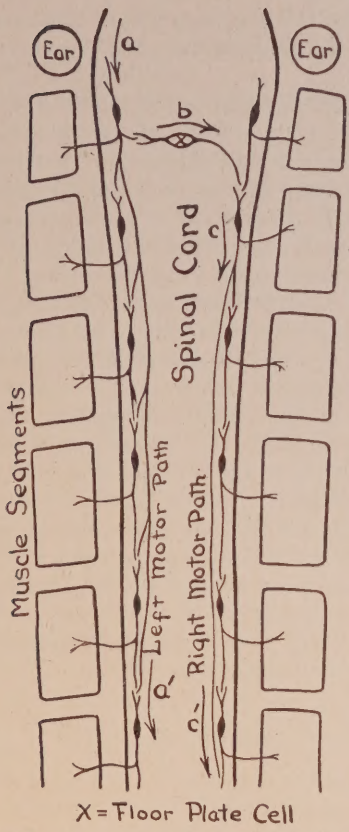

FIG. 86. — Diagram to show neurone mechanism involved in the swimming reflex (all sensory neurones omitted). The initial impulse travels tailward from *a* to *a'* and beyond, exciting the muscle segments to contraction. At the same time the collateral fibers are excited and transmit this impulse to floor plate cells (x) as at *b*. This impulse now passes tailward from *c* to *c'* along the right motor path. See text for further explanation. (From Coghill, "Anatomy and the Problem of Behavior," by permission of The Macmillan Co., publishers.)

development the nervous system is an integrated whole in which specific reflex arcs are differentiated just as the pattern of behavior is an integrated whole in which separate partial patterns such as those of the limb movements are successively individuated.

Instincts and Intelligence. — The ability of the vertebrates and particularly of man to learn and develop new behavior patterns is due to the fact that the neurones of the vertebrate nervous system continue to grow and develop new synapses after the system is already functioning. The insect, on the other hand, does not possess such reserves of embryonic nervous tissue, and so its behavior is less subject to modification. When it becomes adult its nervous system is complete, and apparently the neurones undergo no further growth. The behavior of the insect, like that of most, if not all, invertebrates, is therefore fixed, or as it is more generally called, instinctive. It should be remembered, however, that it is exceedingly difficult to distinguish between chain reflexes established by continued usage and those performed for the first time without any practice whatever. Only the latter may be called instincts. The account of the way in which the swimming reflex in *Amblystoma* is developed shows that this is not instinctive in the strict sense of that word, but is brought about by continued practice and the progressive parallel expansion of the synaptic network and the pattern of behavior. There is a growing tendency to use the word instinct only with great caution at the present time.

ADAPTIVE RESPONSE

We cannot leave the subject of behavior without reference, at least, to the problem of adaptation, which is thought by some to be one of the properties of organisms. This idea is expressed in the sentence, "plants and animals adapt themselves (or are adapted) to their environment." What is meant by the word *adapt* in this connection? In general, it may be said that responses which are advantageous to the organism are known as adaptive. A more precise statement is that the response of an organism to a change in the environment is adaptive if, because of the response, the organism maintains its existence otherwise unchanged but could not do so unless this response were made. A simple example may be seen in the phototropism of the seedling. The root is negatively phototropic and grows away from

the source of illumination, while the shoot is positively phototropic, growing towards the light. As the root is the absorptive organ and the shoot the photosynthetic organ, this tropism permits the development of essential functions of plant existence, and may be called adaptive.

Yet in other cases of fixed response it is more difficult to see wherein the adaptation exists. Take, for example, the classical reaction of the moth to flame, with its fatal termination. It has been urged that this instinct under ordinary conditions is advantageous, for such positively phototropic response would lead the insect to white flowers in weak illumination and is therefore adaptive.

Adaptiveness a Function of Organization. — It seems to follow from the definition of adaptiveness quoted above that adaptive response is really a function of organization. That is to say, the organism continues to exist only because it is sensitive to changes in the environment and its response to them is determined by the complexity of its organization. According to this interpretation, the pattern of an animal's behavior is the result of the irritability of its protoplasm. The organism nevertheless behaves as a unit in the environment by which it is surrounded and the idea of adaptation is a useful one as applied to the organism as a whole. Care must be taken, however, to avoid all expressions implying any purposiveness on the part of organisms, such as "*Paramecium* backs away from an obstacle *in order to* avoid it." This implication of purpose is known as **teleology** and is vigorously denied by the majority of biologists.

Subjective Phenomena. — With the problems of consciousness, sensation, volition, and the like, the biologist is not directly concerned. They cannot be studied in animals except by the dubious method of ascribing to the manifestations of animal behavior psychological meanings attributed to similar responses in man. One school of psychologists, the behaviorists, are concerned solely with the objective side of that subject, and base their work on the phenomena of the neurone, synapse, and reflex. Others, the mentalists, are concerned primarily with the subjective side of psychology and deal with the phenomena of the mind as an independent subject. But the word "mind" arouses as many problems as does the word "life," and the reader who cares to pursue this subject further is referred to the literature of psychology.

CHAPTER VI

THE CELL AND REPRODUCTION

That new individuals develop only from detached portions of existing organisms is an axiom of modern biology. *Omne vivum*

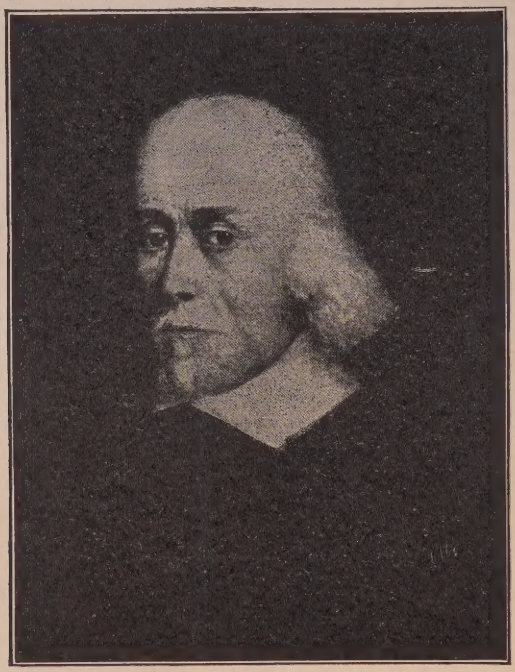

FIG. 87. — William Harvey (1578–1657), an early embryologist, who discovered the circulation of the blood. (From Locy, "Growth of Biology," Henry Holt and Co.)

ex ovo is a Latin aphorism coined to express this law of **Biogenesis,** by Harvey (1578–1657), better known from his discovery of the circulation of the blood. It had formerly been supposed that some forms of life were produced by inanimate matter (**abiogene-**

FIG. 88. — Louis Pasteur (1822–1895), whose studies of fermentation disproved the theory of spontaneous generation (abiogenesis). (From Locy, "Biology and Its Makers," Henry Holt and Co.)

sis). The great Italian biologist Redi in 1688 tested some of the currently accepted notions, such as the origin of maggots from meat, and found, of course, that if the meat were screened from flies, no maggots developed. He demonstrated that these were but the larvae of flies developing from eggs laid by the flies on the exposed meat. Later Pasteur (1822–1895) in a brilliant series of experiments refuted the idea that micro-organisms (bacteria and fungi) could arise by spontaneous generation. Such ideas die hard, however, and many today probably believe that the thread worm (*Gordius*, Fig. 175) found in watering troughs is a living horse hair. And at least one book has been written in our own day to prove that under certain circumstances living protoplasm can be generated in complex chemical solutions. It is always possible that this might be accomplished, but in view of the complexity of what we call protoplasm (Chapter IV), it is doubtful whether it has been or will be done in our time.

Two main types of reproduction are recognized. In **asexual** reproduction, the detached portion (large or small) of the parental organism develops directly into a replica of the parent. In **sexual** reproduction the detached portions are single cells, which normally must unite in pairs to become the germ of the new organism.

ASEXUAL REPRODUCTION

Like metabolism and irritability, reproduction is a characteristic of the cell. Whether a free-living organism or part of a multicellular body, the cell has arisen from a pre-existing cell, and under ordinary circumstances will give rise to others. No cell has ever been known to arise in any other way.

Cell Division. — The reproduction of the cell is ordinarily asexual and in some cases entirely so. It is initiated by the division of the nucleus, which may be performed in one of two ways.

Amitotic Division. — The older biologists recognized the division of the nucleus prior to cell division but did not observe the finer details of the process, and thought it to be a relatively simple affair, in which the nucleus underwent a constriction which separated it into two equal halves. It is now a matter of general agreement that this simple, amitotic division is relatively infrequent, and that cells originating through **amitosis** (Fig. 89) cannot reproduce themselves except in this way. Amitotic division is sometimes confused with nuclear fragmentation.

This is simply an exaggerated form of nuclear branching in which the branches actually separate from the central mass but recombine with it prior to what is ordinarily a mitotic division.

Mitosis. — In **mitosis,** the more usual type of cell division, the division of the nucleus is preceded by the formation of long slender threads of chromatin called chromosomes. These are ordinarily constant in number within a species. With certain important exceptions to be considered later, every cell in a given species will have the same number of chromosomes formed in every cell division. And again with exceptions to be noted in a later chapter, this number is an even one. Prior to the actual division of the cell, each chromosome is divided longitudinally in such a way that each of the daughter cells will have one half of each of the original chromosomes. In this way the number of chromosomes is kept constant from cell to cell. Thus the number of chromosomes in man seems to be 48, although some observers have reported 24. The smallest number (2) is found in one variety of a parasitic worm,[1] while the largest number reported is 200 in the crayfish.[2] Although the number of chromosomes is constant, the individual chromosomes often differ from each other in appearance and can be identified in successive divisions. They have been seen in the living cell but are ordinarily studied in cells which have been killed, cut in thin sections, and stained so that their microscopic anatomy may be preserved and examined at a higher magnification.

FIG. 89. — Stages in amitosis as seen in the tendon cells of a new-born mouse. *nc.*, nucleolus. (After Nowikoff, from Kellicott, "General Embryology," Henry Holt and Co.)

Plant Mitosis. — Although the process of mitosis is a continuous one, certain stages are conspicuous and are helpful in describing other phenomena of reproduction. These are brought out in the accompanying figures of mitosis in the onion root tip.

In the first stage, the **prophase** (2–5, Fig. 90), the chromatin granules unite in a long coiled thread called the **spireme.** This spireme is then split longitudinally into two threads which remain closely applied to each other. The thread then shortens

[1] *Ascaris megalocephala univalens.* [2] *Cambarus virilis.*

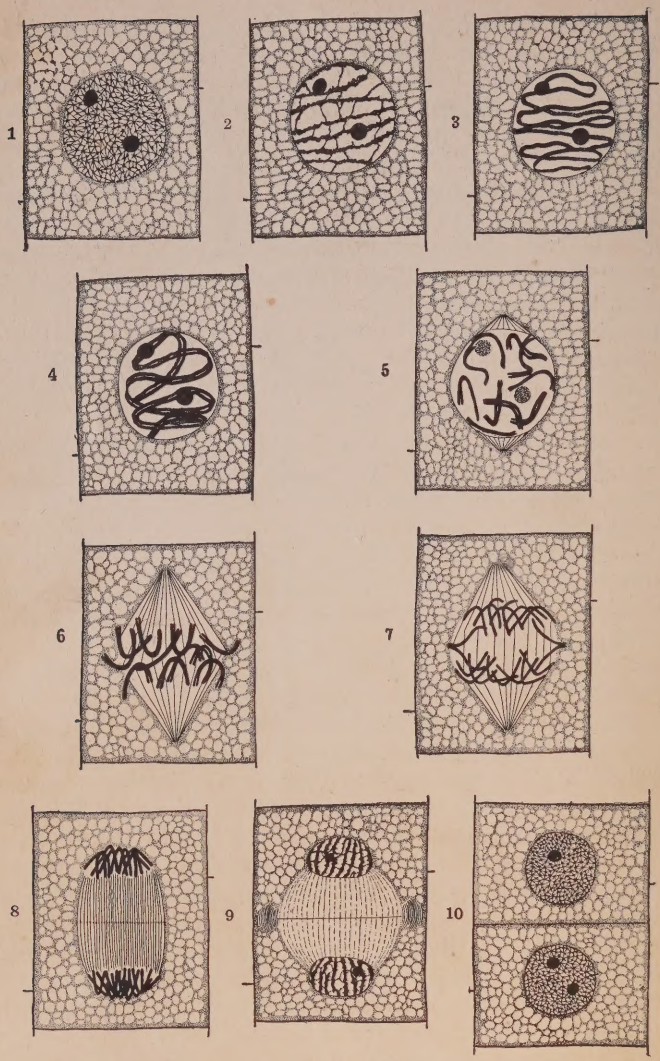

FIG. 90. — Diagrams to show stages in mitosis as seen in root-tip of onion (*Allium cepa*). 1, Before mitosis; 2, prophase; 6, metaphase; 7–8, anaphase; 9, telophase; 10, daughter cells after mitosis. Note formation of spireme (3), absence of centrosomes, and cell plate (8, 9). (From Holman and Robbins.)

and segments into a series of rods, each of which is still double. These rods are the chromosomes, and in the onion number 16. Following the appearance of the chromosomes the nuclear membrane is dissolved, and in the space which it formerly occupied two cones of delicate fibers, diverging from centers on opposite sides of the nucleus, come together to form a **spindle** lying in the long axis of the cell. Some of the fibers attach themselves to chromosomes; others extend from pole to pole.

The chromosomes now take up a position across the middle of the spindle and form what is called the **equatorial plate.** They are now said to be in the **metaphase** (6, Fig. 90). The metaphase is of relatively short duration, but during this period the chromosomes may be stained most intensely, probably because of their greater compactness.

In the following stage, the **anaphase** (7–8, Fig. 90), the chromosomes separate into the two longitudinal halves of which they are composed, each daughter chromosome moving toward one pole of the spindle or the other, exactly as though they were pulled by the spindle fiber attached to each.

Following the anaphase comes the **telophase** (9, Fig. 90), in which each set of daughter chromosomes disintegrates into its constituent granules while a nuclear membrane forms around each set. Swellings now appear on each of the fibers of the spindle at the equator. These unite to form a **cell plate** which extends across the cytoplasm and finally splits to become a part of the plasma-membrane of each daughter cell. With the disappearance of the spindle and the deposition of cellulose to form new cell walls between the daughter cells, each is now reorganized exactly like the parent cell. The appearance of the spireme as a *linear* series of chromatin particles and the *longitudinal* split by which each particle is divided seem to be the essential features of mitosis.

Mitosis in the Animal Cell. — In the division of the animal cell (Fig. 91) the centrosome (not found in the cells of flowering plants) divides in the prophase, and the two daughter centrosomes move apart as the spindle forms between them. The fibers instead of being restricted to the spindle diverge in all directions, thus forming **asters,** which radiate often to the periphery of the cell. The chromosomes are formed simultaneously but separately instead of originating in a continuous spireme. No cell plate is formed, but, as the cell wall is not stiffened with cellulose, the cytoplasm rounds up about each centrosome as a center.

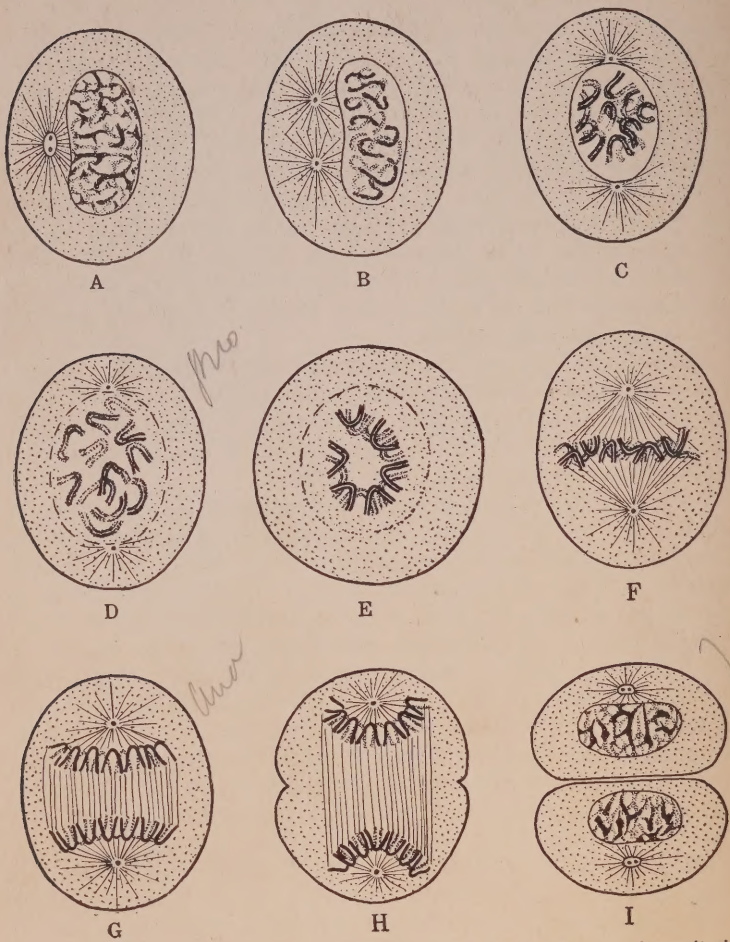

FIG. 91. — Diagrams to show stages of mitosis in an animal cell. A, before mitosis; B, C, D, prophase; E, metaphase to show equatorial plate; F, metaphase in side view; G, H, anaphase; I, daughter cells after telophase. Note centrosomes, absence of spireme, and absence of cell plate. (After Corning, from Shumway).

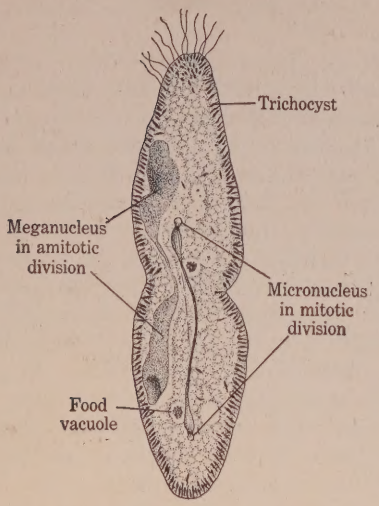

FIG. 92. — *Paramecium caudatum*, longitudinal section of dividing individual. (After Calkins.)

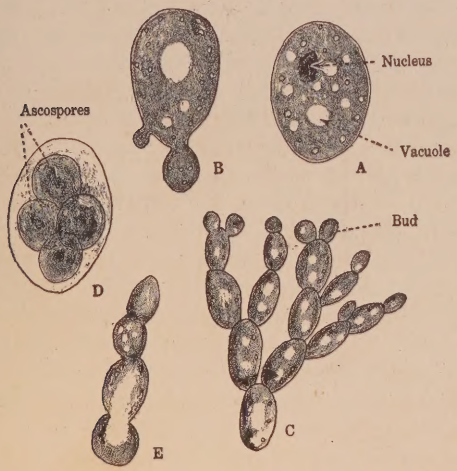

FIG. 93. — Yeast (*Saccharomyces cerevisiae*); A, single cell; B, budding cell; C, chain of cells produced by budding; D, spore formation; E, spore germinating and budding. (After Curtis, from Holman and Robbins.)

This produces an **equatorial furrow** and division by constriction follows.

Types of Asexual Reproduction. — Free-living cells also reproduce themselves by division. This division is usually into two equal halves (**binary fission**), as in the case of *Paramecium* (Fig. 92). This protozoan like all the ciliates has two types of nucleus, a larger **meganucleus**[3] and a smaller **micronucleus.** It will be noted that the meganucleus divides amitotically while the micronucleus divides by mitosis.

Gemmation. — In other types the division may be unequal so that smaller cells seem to be budded from the parent (**gemmation**). This is seen for example in the reproduction of the unicellular plants called yeasts (Fig. 93, *B, C, E*), where not infrequently several buds are formed at the same time. In unequal division of this type the proportions are determined by the position of the nucleus. If this is in the center of the cell the division is equal, but if it is nearer the surface the division is unequal. Thus it will be recalled that, in the unequal division of the frog's egg which gave rise to the polocytes, the nucleus was very close to the plasma-membrane.

Sporulation. — The formation of several buds before they are detached from the parent cell if carried still further results in a phenomenon known as spore-formation (**sporulation**) (Fig. 93, *D*). Here the nucleus divides several times before any division of the cell body takes place, so that a large number of small cells called **spores** are formed simultaneously, when the cytoplasm about each daughter nucleus is split off from the rest. This is well seen in the life history of the sporozoön *Menocystis* (Fig. 94).

Variations. — In all these cases the division of the nucleus is mitotic, although the details of the process may vary from the two types described above. Thus in the bacteria, which lack a formed nucleus, but have granules of chromatin scattered throughout the cell body, the chromatin aggregates before division, and it is believed that the several particles divide independently. But nothing is known as to the method of segregation of the daughter particles between the dividing halves of the cell. Many interesting variations of mitotic division are to be observed among the unicellular plants and animals, for an account of which the student is referred to textbooks of botany and zoölogy, respectively. In many cases, prior to fission or sporulation, the

[3] I prefer this word to the more commonly used "macronucleus" as it is not so easily confused with "micronucleus."

cell rounds up, some of the differentiated organelles disappear, and the cell secretes a wall about itself known as a **cyst** (Fig. 94, *I*).

Growth. — The phenomena of binary fission, gemmation, and sporulation are found in unicellular plants and unicellular animals. In all of these the germ, as we may call the product of

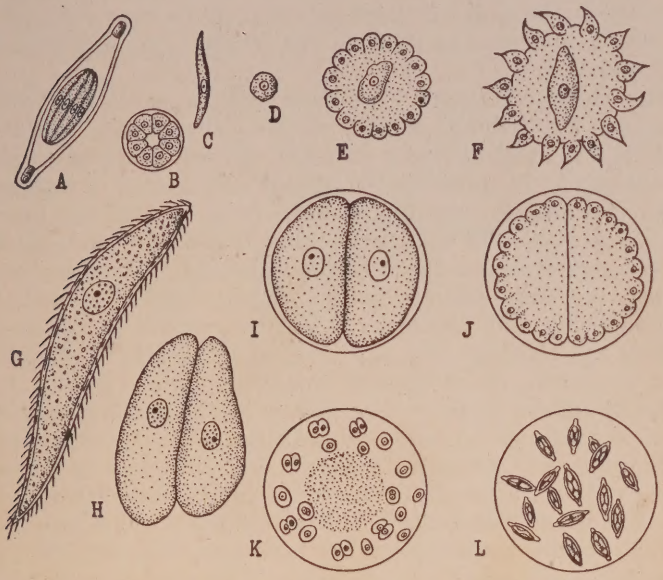

FIG. 94. — Life cycle of *Monocystis*, a parasitic protozoön. A, spore case with eight sporozoites; B, same in cross section; C and D, free sporozoites; E, F, G, stages in the transformation of sporozoite into trophozoite within a sperm-sphere of earthworm; H, union of trophozoites; I, encystment; J, gamete-formation; K, syngamy; L, formation of spore case and division of zygote into sporozoites. (From Curtis and Guthrie.)

cell division, soon grows until it has attained the size of the cell by which it was produced. During this period the constructive, anabolic processes of the cell exceed the destructive processes of catabolism. In other words, protoplasm is being built up faster than it is broken down, and provided that an excess of food is present the cell increases in size. One of the older distinctions between living and non-living objects was the alleged difference between growth by **intussusception** (the weaving of new materials

into the very fabric of the cell) and growth by **accretion** (adding to the structure at the surface). The explanation of this difference, however, is simply that the very complexity of protoplasm and the fact that foreign material is taken in only through the semipermeable membrane necessitate that growth come from within. Once within the plasma-membrane there is no reason to suppose that new material caught up in the metabolism of the cell may not be added to existing materials or even structures by the simple process of accretion. The difference appears to be one of complexity.

The Limits of Growth. — A more difficult question, however, is that of the limits of growth. If the cell is capable of growth and food is available, why does not the cell continue to grow indefinitely? We know very well that cells as well as organisms have very definite size limits. The largest organisms known, past or present, are the Big Trees of California[4]; the smallest visible organisms are the bacteria, unicellular plants which approach the limits of microscopic visibility at 0.2 micron, the micron being .001 millimeter. The largest cell known is the ostrich egg, although this was exceeded by the egg of an extinct bird, *Aepyornis*, whose egg-shell has a capacity of a gallon.

Surface-Mass Ratio. — One factor in the limitation of cell size is the ratio of the surface to the mass. The surface increases as the square of the radius, while the mass increases as the cube of the radius. Since all the necessary interchanges between the cell and its environment take place at the plasma-membrane, continued growth will disturb this ratio and, therefore, the equilibrium of metabolism. To be sure, the amount of surface may be increased by wrinklings, projections, etc., but even so growth cannot continue indefinitely.

Vegetative Reproduction. — In the less highly organized multicellular organisms, portions of the body may be detached which develop into replicas of the parental stock. We have already seen how in the wheat, branches of the shoot give rise to several sporophytes (tillering). Many plants reproduce to a greater or less extent by budding, an asexual process which the botanist describes as **vegetative** reproduction. These buds may arise on the root (**suckers**) or on the stem (**runners**). From these the new organisms arise by growth of the individual cells, continued cell division, and a process of cell specialization, known as **differentiation,** to which we shall refer in a later section of this chapter.

[4] *Sequoia gigantea.*

Budding. — Asexual reproduction of this type is common among the less highly organized animals. It is sometimes the case that the division is equal, as in the case of the flatworm *Planaria*, and rarely in *Hydra*. More frequently, as is generally the case in the latter type, the division is unequal, that is to say, it results in budding. In *Hydra* (Fig. 95), endodermal cells push

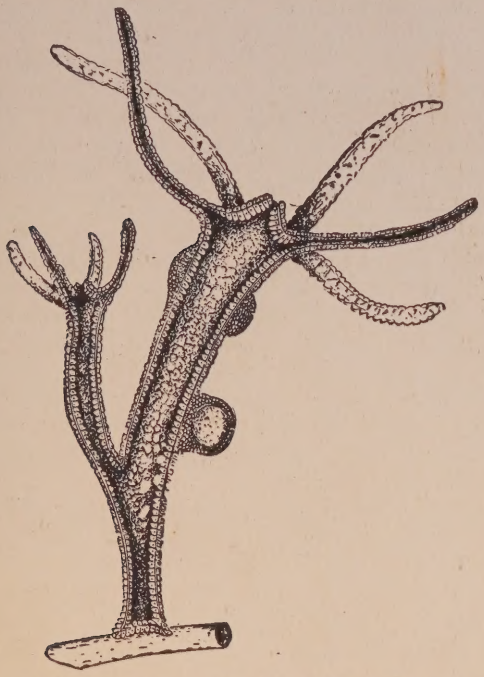

FIG. 95. — *Hydra* in reproduction. Note bud at left, testes on main stem below tentacles, and ovary at right opposite bud. Optical section. (From Calkins, "Biology," Henry Holt and Co.)

out from the gut to form a blind pocket lined with endoderm and covered with ectoderm, protruding from the body of the parent. Tentacles develop on the apical end, and a constriction at the basal end results in the detachment of a miniature replica of the original organism.

Colony Formation. — Among both unicellular and multicellular plants and animals, the new individuals often fail to separate completely from the parent. This results in the appearance of

colonies, which may consist of similar individuals, or of individuals so specialized for separate functions that it is hard to say whether the aggregate is a colony or an individual. (See page 146.)

Regeneration. — Asexual reproduction is closely allied to the phenomenon known as **regeneration,** which is the reproduction of a part of the organism only. Even unicellular organisms such as *Paramecium* have this ability, for it has been shown that if this organism is cut in pieces, each piece may reorganize into a complete individual, providing a micronucleus is present.

The power of regeneration is closely associated with that of asexual reproduction, the difference between the two being that in asexual reproduction an entire new individual is reproduced, while in regeneration the missing portion only of an existing individual is regenerated. It is, therefore, to be expected that organisms which have the power of asexual reproduction should also be notable for the ability to regenerate missing parts, whereas those forms which reproduce only by sexual methods should have smaller regenerative powers. Furthermore, the less highly organized animals have the greater capacity for regeneration.

Among the higher plants, stem cuttings, that is to say, pieces of stems, when placed in moist soil will often develop roots and leaves like Aaron's rod. Leaf cuttings and pieces of root sometimes show this same phenomenon.

Hydra shows a very complete power of regeneration as well as asexual reproduction of new individuals. It is able to regenerate complete individuals from the several fragments after having been cut into two or even more pieces. This process involves first what has been called **de-differentiation;** the cells nearest the injured region lose some of their specialized characteristics and take on the appearance of embryonic cells, preparatory to a period of intensive division. Secondly the cells rearrange themselves so that the form of the *Hydra* is restored; this is called **moulding.** Finally the cells differentiate again into the forms and functions appropriate to the tissues of the regenerated part, and with continued growth and division, regeneration is complete.

Healing. — This power of regeneration is lost progressively with the increased organization of higher forms. The tadpole can regenerate a part of the tail or leg, but the adult frog has little power of regeneration and cannot develop even a new finger or toe. The human species has largely lost the capacity for regeneration except as seen in the healing of injured surfaces.

Grafting. — Closely related to regeneration and healing is the phenomenon of **grafting.** In this, parts of one individual are attached to another in such a way that the cut surfaces unite and the attached portion cuts in on the vascular system of the host. Grafting is a common practice among horticulturists, either as stem grafting, in which a stem cutting (**scion**) is grafted upon a **stock,** or as bud grafting, in which a bud is used. Portions of early frog embryos have been successfully grafted on others, and even in man, skin grafting and blood transfers are successful procedures.

Tissue Culture. — Asexual reproduction in all its varied forms, and the allied phenomena of regeneration, grafting, and healing, demonstrate the ability of the cell either as an independent organism or as a component of some cellular organization to maintain its existence and reproduce itself under favorable circumstances. Nowhere is this better shown than in what is known as tissue culture. Bits of tissue taken from any organism, including the human body, under aseptic conditions, and, placed in a suitable nutrient medium, may be kept alive for an indefinite period, provided that the waste products of metabolism are removed and fresh nutriment added by changing the medium at appropriate intervals. *Paramecium* has long been a favorable object for the study of longevity in protozoan protoplasm, and Woodruff has continued a strain[5] in the laboratory for over twenty years, during which time over 12,000 generations have been produced. Many of the higher plants, such as the fig tree, have been preserved for centuries by vegetative reproduction alone. Cancerous tissue has been maintained in the bodies of rats for over ten years by removing a bit of the growth and transplanting it into the body of a new host, and much information of value is being learned from the continued study of this pedigreed stock.

In the great majority of organisms, however, the asexual reproduction of the cell by division is interrupted by sexual reproduction.

SEXUAL REPRODUCTION

In sexual reproduction there is usually an exchange of material between two individuals which differ from each other in certain respects. The nature of the difference is not clearly understood, but its existence is recognized in the use of the word **sex.** In the unicellular organisms there is either a complete and permanent

[5] *Paramecium aurelia.*

fusion between the cells concerned, or a partial and temporary fusion between the cells, while an exchange of nuclear material is made. The fusing cells are called **gametes,** the act of fusion is known as **syngamy,** and the product of this union is termed a **zygote.** Under certain conditions a gamete may give rise to a new individual without undergoing syngamy. This act is known as **parthenogenesis.** In both syngamy and parthenogenesis there is a breaking down and reorganization of the structure of the gamete prior to further development. In this process the behavior of the chromosomes is both striking and significant. In the multicellular organisms, the gametes are highly specialized cells, eggs and sperm, which unite in fertilization (syngamy) to form a fertilized egg (zygote). The egg will under certain conditions undergo further development even though unfertilized (parthenogenesis). Chromosome reduction takes place at some time in the life history prior to gamete formation. We may now examine a few cases of sexual reproduction in greater detail.

Syngamy. — We have already had occasion to examine the process of sexual reproduction in the frog and the wheat with their highly specialized gametes (egg and sperm) and syngamy (fertilization). Among the unicellular plants and animals, we shall find similar phenomena.

Isogamy. — In *Ulothrix* (Fig. 96), we see an example of a unicellular plant which reproduces both asexually and sexually. *Ulothrix* is colonial, and the colony is composed of cells united end to end, forming an unbranched filament. A single basal cell is specialized as a **holdfast.** It is longer and narrower than the other and has no chloroplast. In asexual reproduction, a single cell will round up within the cell wall, develop four flagella and escape as a motile spore (**zoöspore**). Sometimes one or more divisions may be undergone before emerging, in which case the cell may give rise to as many as eight such spores. These swim about for a time and then settle down, secrete a cell wall and reproduce a new colony by cell division.

In sexual reproduction, the vegetative cells produce motile spores which are smaller, more numerous (as many as 32 from a single cell), and have but two flagella instead of four. These spores are the gametes, known as **isogametes** because both members of a conjugating pair are of the same size. They are incapable of further development unless a gamete from one filament encounters a gamete from some other filament, in which case they fuse to become a zygote (**zygospore**). This secretes a

cell wall but does not undergo further development (germination) for a considerable period of time until conditions are again

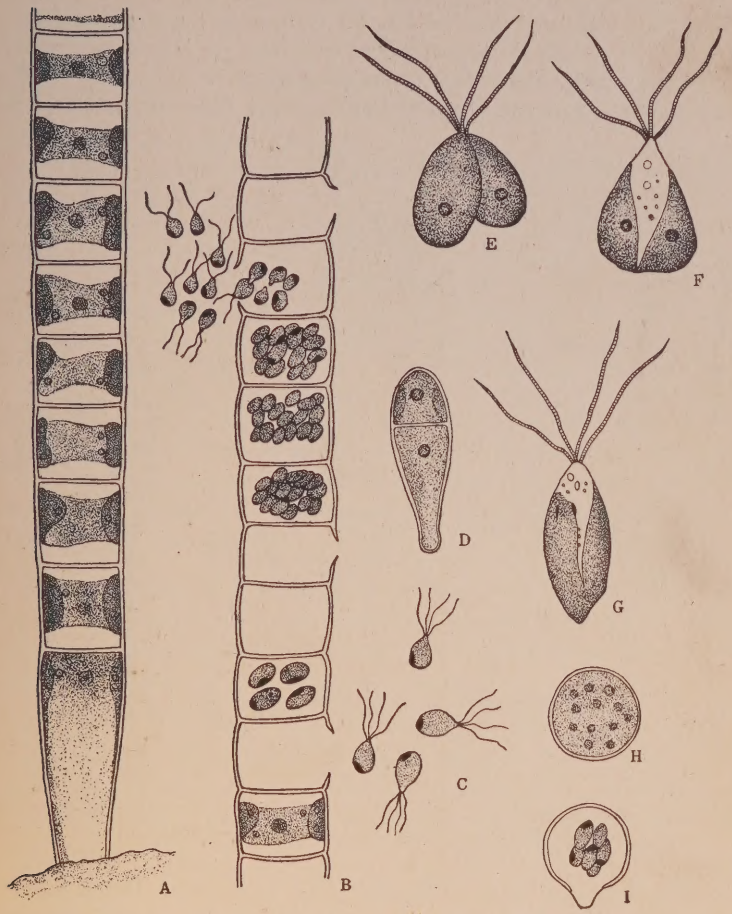

FIG. 96. — *Ulothrix zonata.* A, part of filament with holdfast; B, same showing formation of gametes (above) and zoöspores (below); D, germinating zoöspore; E, F, G, syngamy; H, zygospore; I, germinating zygospore. (From Holman and Robbins.)

favorable for vegetative existence. At that time it emerges as a zoöspore. It may undergo a number of divisions prior to this time so that several zoöspores are formed. Exceptionally a

gamete may secrete a cell wall and give rise to a zoöspore without previously fusing with another gamete (parthenogenesis).

Anisogamy. — In another green unicellular plant, *Oedogonium* (Fig. 97), asexual reproduction by zoöspores takes place as in *Ulothrix*, but gamete formation is restricted to specialized cells, and the gametes are of two types (**anisogamy**). The cells which produce male gametes are called **antheridia**; the male gamete is a

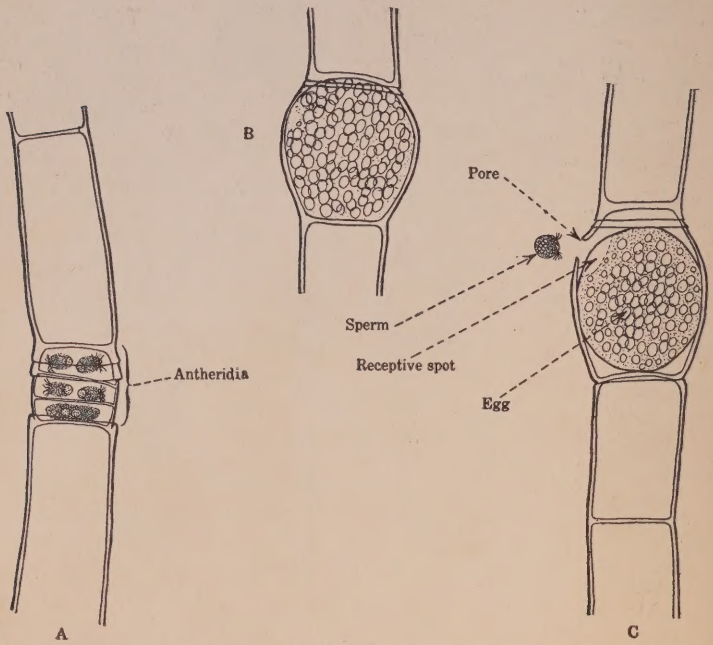

FIG. 97. — *Oedogonium*. A, portion of male filament; B, part of female filament; C, just before syngamy. (From Holman and Robbins.)

small motile cell with a ring of cilia, resembling the zoöspore except in size. The female gamete is produced by a cell known as the **oögonium** (not to be confused with the oögonia of the metazoan ovary described on page 38). The protoplasm in each oögonium enlarges and rounds up to form the egg. Opposite a clear area (the receptive spot) a pore is formed in the wall of the oögonium through which the sperm enters to fertilize the egg. A thick wall is formed about the zygote. Before germination

the nucleus of the zygote, which contains two sets of chromosomes, one from each gamete, divides twice, and four zoöspores are formed. In one of these divisions the number of chromosomes is reduced from the double number to that characteristic of the species at all other times. We shall have occasion to refer to this reduction in chromosome number frequently hereafter. If it were not for this, the number of chromosomes would be doubled at each generation.

Conjugation in Paramecium. — Sexual reproduction in this form is represented by a temporary and incomplete fusion of the conjugating individuals which differ only slightly in size. They approach each other and become attached along the anterior third of the body. The meganucleus of each disintegrates while the micronucleus divides twice, producing four daughter micronuclei (Fig. 98, *A–E*). One of these divides again to form two **pronuclei** (Fig. 98, *F*) of which one migrates into the other *Paramecium* and fuses with one of the pronuclei in that cell, while a migratory pronucleus from the second *Paramecium* enters the body of the first to make a reciprocal union (Fig. 98, *G*, *H*). The other micronuclei disintegrate. The conjugating forms then separate and the two **exconjugants** reorganize their protoplasm according to a complicated process in which the fused pronuclei divide three times, forming again eight nuclei, of which four remain as micronuclei while the others pair up with them and become meganuclei (Fig. 98, *I–M*). The cell then divides twice giving rise to four daughter cells each with a meganucleus and micronucleus (Fig. 98, *N–P*).

It must be noted that there are two different kinds of nuclear division seen in this process. The first two divisions of the micronucleus are equal. The third division is unequal, as it gives rise to a larger stationary pronucleus and a smaller migratory pronucleus. These are comparable to the gamete nuclei of other organisms. The product of the fusion of a stationary and a migratory pronucleus may therefore be considered the zygote nucleus.

Parthenogenesis. — That the act of conjugation or fertilization is not absolutely essential to the continued existence and development of the gamete is indicated by the existence of parthenogenesis. This type of reproduction, in which a sexual gamete gives rise to a new individual without syngamy, occurs naturally in some unicellular plants like *Ulothrix*, as an exception to the more usual mode of reproduction in which syngamy is the rule.

Endomixis. — Conjugation is not a periodic or even a necessary phenomenon in *Paramecium*. In Woodruff's strain of *Paramecium*, already referred to, over 12,000 generations were produced without conjugation. During this time he discovered

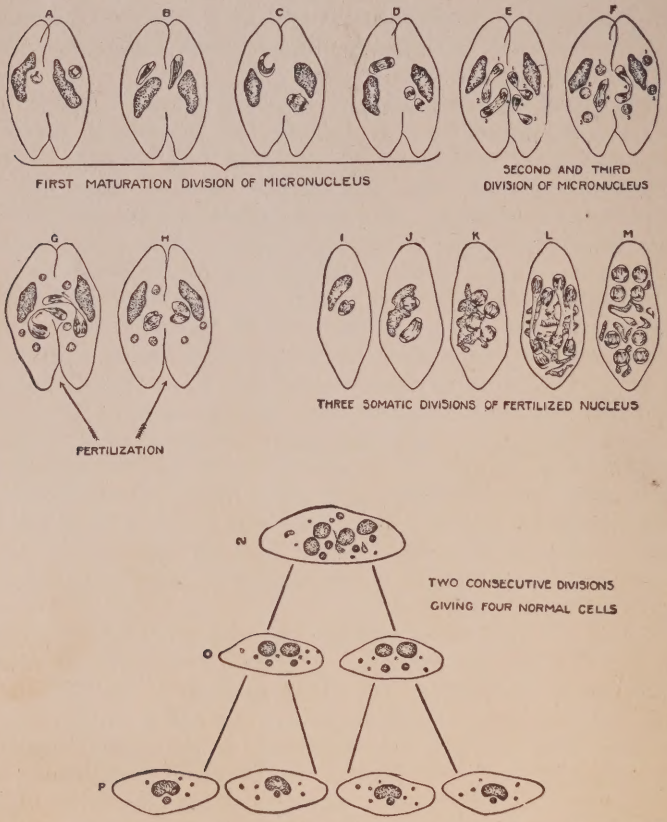

FIG. 98. — Stages in conjugation as seen in *Paramecium caudatum*. (From Calkins, "Biology," Henry Holt and Co.)

that periodically the *Paramecia* underwent a period of reorganization comparable to the preliminary stages of conjugation. But as there exists no possibility for the exchange of nuclear material, the final division which in conjugating individuals separates a migratory pronucleus from a stationary pronucleus

is omitted. The cell therefore is reorganized, using this undivided daughter micronucleus instead of the fused pronuclei as a starting point. This phenomenon (**endomixis**) may be compared with parthenogenesis, just as conjugation in these ciliate protozoa may be compared with fertilization.

Parthenogenesis in Higher Organisms. — Among the multicellular plants and animals, parthenogenesis is not uncommon. It is seen even among the flowering plants and is well known among worms and insects. Two main types are to be distinguished. In the first type, both maturation divisions are undergone by the developing eggs. These give rise to males if un-

FIG. 99. — *Apis mellifica*, the honey bee. a, worker or sexually immature female; b, queen or sexually mature female; c, drone or male. (From Curtis and Guthrie.)

fertilized, and females if fertilized, as is the case in the bees (Fig. 99). The developing sperm, however, have only a single maturation division.

In the second type of parthenogenesis, the egg undergoes only a single maturation division as in certain insects and worms. In some cases as in the plant lice, e.g., the rose aphid,[6] parthenogenetic and syngametic generations succeed each other in a sort of alternation of generations. (See next page.) During the greater part of the summer, only females are found. These lay eggs which, without fertilization, develop, after a single maturation division, into females. After several parthenogenetic generations, some of these eggs develop into males in the late summer. The corresponding female generation produces eggs which undergo

[6] *Macrosiphum rosae.*

both maturation divisions and will not develop further unless fertilized. The fertilized egg gives rise to parthenogenetic females. If the aphids are kept at summer temperatures the sexual generation fails to appear, as it does in some worms and insects, so that males are completely unknown. The result is that what was originally a variant of sexual reproduction has become asexual through the loss of the sex distinction.

Artificial Parthenogenesis. — In artificial parthenogenesis, allusion to which was made in connection with the development of the frog, the egg is treated with various chemical or physical agents, by which it is stimulated to further development exactly as though entered by a spermatozoön. The end result, however, is parthenogenetic, as there has been no contribution of protoplasm from a male parent.

Alternation of Generations. — In the unicellular forms just described, we have noted that both asexual and sexual reproduction occurs, and that the asexual mode is the general one while sexual reproduction takes place only occasionally. Among many of the multicellular plants and animals such alternation of generations takes place, and the sexual and asexual generations often differ from each other greatly in appearance.

Life History of Wheat. — We have already seen in the development of the wheat that the pollen and ovules, once thought to be germ cells like the sperm and eggs of animals, are in reality spores of two kinds (microspores and megaspores). These give rise to parasitic sexual plants, the pollen tube and embryo sac, and the sperm nucleus formed by the one and the egg nucleus formed by the other are the pronuclei by whose union arises the nucleus of the zygote from which the new sporophyte is produced.

Life History of a Moss. — In less highly organized plants, the mosses, it is the sexual generation which is more conspicuous. The moss plant (*Funaria*) (Fig. 100) is made up of leafy shoots with thread-like roots (**rhizoids**). In reality these plants are branches (**gametophores**) of the true gametophyte, which is a branching green filamentous structure, the **protonema,** much like a branching alga. The rhizoids absorb water and salts, while the leafy shoots and protonema are photosynthetic. At the ends of these shoots are produced **antheridia** and **archegonia,** which give rise to sperm and an egg, respectively. During a wet period the sperm escape from the antheridia and swim to the archegonium, which they enter to fertilize the egg. The zygote,

still within the archegonium, secretes a wall of cellulose, and by growth and repeated cell divisions becomes the embryo of the sporophyte. It differentiates into three portions: a **foot** (compare the root of the wheat sporophyte), **seta** (or shoot), and **capsule** (spore-forming organ, compare sporophylls of wheat). The foot penetrates the tissue of the gametophore from which it absorbs its food in parasitic fashion. The seta lengthens rapidly.

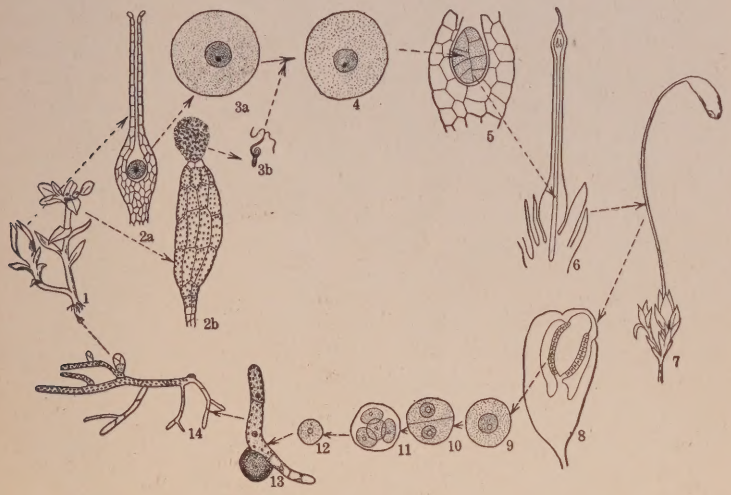

FIG. 100. — Diagram to show life history of *Funaria*, a moss. 1, gametophore with antheridial (right) and archegonial (left) branches; 2a and 3a, archegonium and egg; 2b and 3b, antheridium and sperm; 4, zygote; 5, embryo sporophyte in archegonium; 6 and 7, developing sporophyte; 8, capsule of sporophyte showing spore mother cells; 9, spore mother cell; 10, 11, maturation divisions of spore mother cell; 12, single spore; 13, germination of spore; 14 protonema. (From Holman and Robbins.)

Within the capsule, spore mother cells produce the spores after undergoing two divisions, in one of which the number of chromosomes is reduced. The spores, disseminated by air currents, germinate to form new protonemae. In some mosses the protonema produces gametophores which bear only antheridia or archegonia. Such a species is called **dioecious.** In *Funaria*, however, a single gametophore bears both antheridia and archegonia, so that this genus is **monoecious.** A further discussion of alternation of generations will be found in Chapter X.

Life History of Obelia. — Alternation of generations occurs also in animals and often involves an alternation between a sessile or attached asexual generation and a free-swimming sexual generation, as in *Obelia*, a colonial relative of *Hydra*. Here the buds produced asexually become either *Hydra*-like **hydranths**

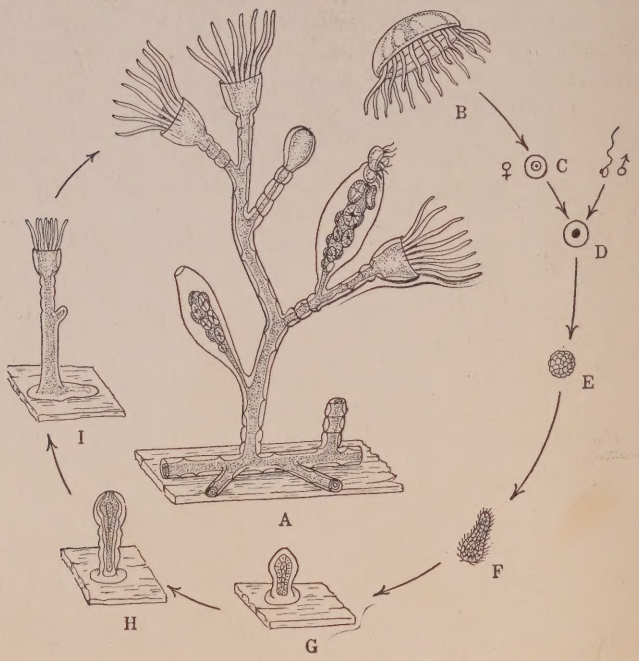

FIG. 101. — Diagrams to show life history of *Obelia*, a colonial relative of *Hydra*. A, colony showing hydranths above, and blastostyles (reproducing individuals) below; B, medusa after escape from blastostyle; C, egg (left) and sperm (right); D, zygote; E, cleavage; F, planula (ciliated larva); G, H and I, stages in development of colony from attached planula.

(feeding individuals) or **blastostyles** (reproducing individuals). The latter give rise to buds which detach themselves as free-swimming **medusae** (jelly fish) and develop either ovaries or testes. The zygotes develop into ciliated larvae (**planulae**) which eventually attach themselves to the bottom and initiate new colonies by budding. The colony perishes after it has given rise to its crop of medusae, and these die after discharging their gametes.

Alternation between sexual and asexual generations is common only among the less highly organized animals, but an alternation between parthenogenetic and syngametic generations has already been mentioned. In this connection attention should be called to the fact that in some animals larval stages may reproduce themselves, a phenomenon known to biologists as **paedogenesis.** An example of paedogenetic reproduction is seen in the life history of the liver-fluke, a parasitic worm with a rather complicated life history, which is to be described in a later chapter (page 267).

Sex Differentiation. — The distinction between egg-producing and sperm-producing individuals in the same species has been noted in some of the preceding paragraphs, and attention was called to the fact that some individuals produced both eggs and sperm. This condition is known as **hermaphroditism;** the individual concerned is an hermaphrodite, and the species is hermaphroditic. A species composed of individuals which produce either male or female gametes is said to be dioecious. Some confusion in terms may arise here from the fact that the zoölogist speaks of an hermaphroditic species as monoecious while the botanist reserves that term for plants which produce both eggs and sperms *but in different flowers* (staminate or pistillate). In the corn, for example, the tassel is staminate (male) while the young ear is pistillate (female). The wheat is hermaphroditic, while the cottonwood and date palm are good examples of dioecious plants.

In many hermaphroditic plants and animals (including the monoecious plants) either self-fertilization or cross-fertilization is possible. In others, such as the earthworm, cross-fertilization only is the rule.

Secondary Sexual Characteristics. — Males and females differ from each other primarily in their capacity for producing eggs or sperm, but in the more highly organized species, many secondary sexual characteristics are frequently developed. In birds (Fig. 102), the difference in plumage of the two sexes is often quite marked.

Gynandromorphs. — An interesting type of sexual anomaly is the so-called **gynandromorph,** which shows male secondary characters in part of the body and female secondary characteristics in another. These have been studied in connection with the inheritance of sex and will be considered later (page 175).

Sexual Endocrines. — In vertebrates the secondary characteristics of sex are profoundly influenced by the endocrines secreted

by the sex glands, so that a reversal of these characteristics may be brought about by a removal of the glands (**castration**) or the transplantation of the glands of the opposite sex. Through the effect of these endocrines the metabolism of the body and the activities of the autonomic nervous system also differ in the two sexes, so that the behavior of the male and female may be markedly affected.

Adaptive Significance of Sex. — It is apparent that sex is not an essential feature in the reproduction of organisms. Many plants and animals reproduce themselves solely by asexual methods or by parthenogenesis, which is to be considered a reversion from a sexual to an asexual method. The essential fact of reproduction is simply that an organism detaches a portion of

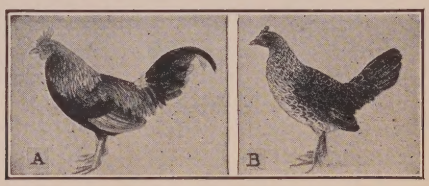

FIG. 102. — *Gallus bankiva*, the jungle fowl to show sexual dimorphism. A, male; B, female. (After Davenport, from Curtis and Guthrie.)

its protoplasm which, alone or after fusion with another detached portion, develops into an organism similar to the parent stock.

Many theories have been developed to account for the existence of sexual reproduction. According to one the mixture of the protoplasm from two different sources rejuvenates a stock which has become senescent. This is difficult to accept in view of the existence of species which have reproduced their kind for long epochs without such rejuvenation. Another is that in the unicellular forms conjugation arose as a method of protection in unfavorable periods or as a means of dispersal. But this is of adaptive significance in relatively few cases only. The one universal aspect of sexual reproduction lies in the reduction of the chromosomes in maturation and the restoration of the doubled number in fertilization. No matter how great may be the discrepancy in size between microgamete and megagamete, no matter how much or how little protoplasm each contributes to the zygote, a complete set of chromosomes comes from each parent. This phenomenon, known as **amphimixis,** is the mecha-

nism by means of which the heritable characteristics of two parents are passed on to the new generation.

The Reduction of the Chromosomes. — In describing the reproduction of *Oedogonium* (page 141) it was pointed out that the zygote had two complete sets of chromosomes, one contributed by each gamete. Unless this number were reduced at some subsequent time prior to the production of another zygote it is clear that the number would be doubled again each time that syngamy took place. However, this reduction took place in the case of *Oedogonium* during the first two divisions following syngamy. Accordingly the zygote alone has the double (**diploid**) number, while all the other cells formed from it (zoöspore, vegetative cell, and gamete) have the **haploid** number, that is to say, a single set of chromosomes. In most of the multicellular plants, the sporophyte generation arising from the zygote retains the diploid number, and reduction does not take place until the spore mother cell divides twice to form the spores. These spores therefore have the haploid number, as do the gametophytes which they produce and the gametes derived from the latter. In all animals the diploid number is found in all the cells of the body except the gametes. Here the reduction takes place during the two divisions of the germ cells (spermatocytes or oöcytes) by which the sperm or eggs are produced. In all these cases the actual reduction is accomplished during two cell-divisions, which are therefore called the **maturation divisions.**

The first maturation division differs from the ordinary mitotic division in that during the prophase the chromosomes unite in pairs (**synapsis**) (Fig. 103, *C*, *D*). The split, characteristic of all chromosomes in the prophase, then develops so that when the metaphase occurs only half the diploid number of chromosomes may be counted *but* each of these has four parts. There has been no reduction in the sense that any chromosomes have been lost; they have merely united in pairs so that the change in the number of visible chromosomes is called pseudo-reduction, and these bivalent, quadripartite bodies are known as **tetrads** (Fig. 103, *E*, *F*). The first maturation division is sometimes called the **heterotypic** division because of its novel features of synapsis and tetrad-formation. When it is completed, each of the two daughter cells has the haploid number of chromosomes which are now known as **dyads.** These daughter cells again divide so that four cells are now formed, each with the haploid number of single (or **monad**) chromosomes. This division is called the **homoeotypic**

division because of its general resemblance to the ordinary mitotic division. The difference lies in the fact that the split in the dyad chromosomes was really formed in the prophase of the preceding (heterotypic) division. Also these two divisions sometimes succeed each other so rapidly that the telophase of the heterotypic

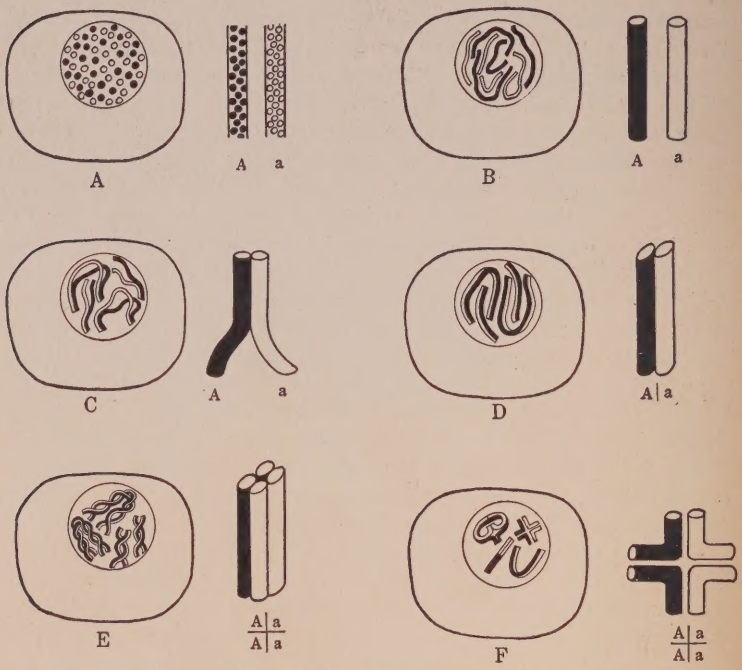

FIG. 103. — Diagrams to show stages in the maturation of the germ cells. Paternal chromosomes (A) are shown solid black, maternal chromosomes (a) solid white. A single pair of chromosomes is shown enlarged to the right of the cell in each stage. A, before first maturation division; B, prophase before synapsis; C, D, synapsis; E, tetrad formation; F, equatorial plate in metaphase of first maturation division. (From Shumway.)

and the prophase of the homoeotypic division are sometimes omitted, and the chromosomes pass from the anaphase of the first division to the metaphase of the second without having undergone the customary disintegration and reorganization.

Origin of the Synaptic Mates. — The chromosomes which unite in synapsis are alike in form and size but differ from each

other in that one was contributed by the egg pronucleus (and hence the mother) while the other came from the male pronucleus

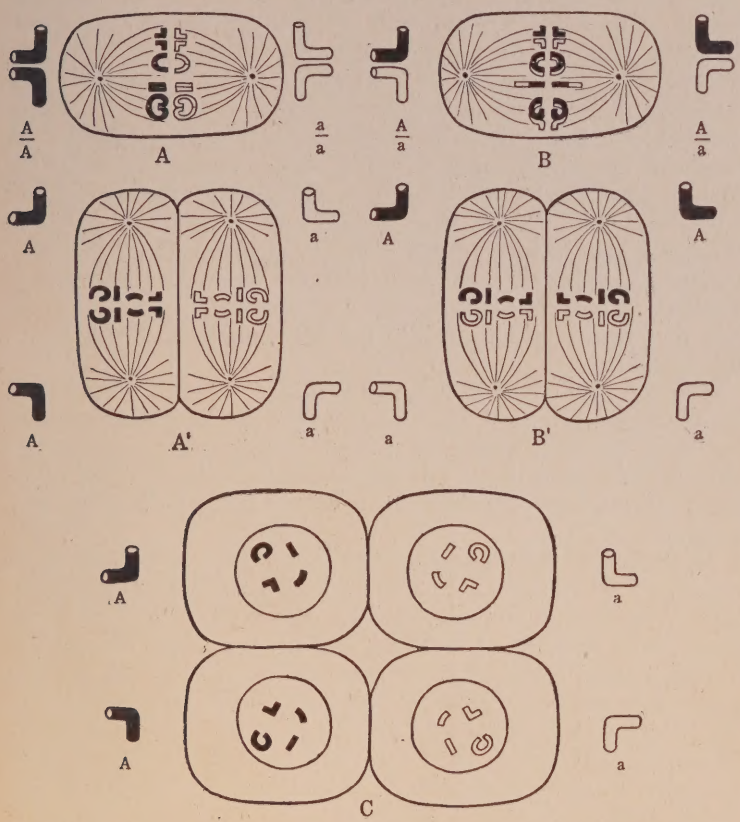

FIG. 104. — Diagrams of maturation. (Continued from Fig. 103.) The distribution of the tetrad $\frac{Aa}{Aa}$ is indicated by the position of the dyads and monads, as the case may be. A and A′, early anaphase of first and second maturation divisions, when the first is a reduction division; B and B′, early anaphase of first and second maturation divisions, when the first is an equation division; C, distribution of the chromosomes in the four gametes after either A′ or B′. (From Shumway.)

(and therefore the father) at the time the individual came into being. We shall refer to the two synaptic mates hereafter as the paternal and the maternal chromosomes, respectively.

Reduction and Equation Divisions. — It is evident that when the tetrad is formed in the prophase of the first division, there are two paternal and two maternal portions. If the division occurs along a plane which will separate the paternal portions from the maternal, the two daughter cells will have, so far as any one pair of chromosomes is concerned, either a paternal or a maternal dyad. Such a division is called a reduction division (Fig. 104, *A*, *A'*). If, on the contrary, the division of the tetrad produces two dyads, each of which has one paternal and one maternal member, nothing has been lost and the division is called equational (Fig. 104, *B*, *B'*). It is extremely difficult to answer the question as to which division, first or second, is the reductional division, for this depends upon how the individual tetrads are severed. The first division may be reductional, equational, or mixed if some tetrads are divided equationally and others reductionally.

The end result is that each gamete has the haploid number of chromosomes (Fig. 104, *C*), part of which are paternal and part maternal, the distribution being entirely according to the laws of chance and probability. The zygote has always the diploid number of chromosomes, including a complete haploid set from each parent.

Reduction in Parthenogenesis. — Attention has already been called to the two types of parthenogenesis based on a difference in the maturation of the egg. In the case of the bees and other forms, both maturation divisions take place, so that the egg has only a haploid set of chromosomes. If unfertilized, the egg develops into a male. His germ cells always undergo both maturation divisions so that the sperm also have the haploid number. If the egg is fertilized, the zygote will have the diploid number and develop into a female. The parthenogenetic egg of the aphid, however, is always produced by a single maturation division which is not reductional so that the diploid number of chromosomes is maintained.

DEVELOPMENT

A single set of chromosomes, the haploid number, is often all that the organism requires for further development, as in the gametophyte, or the drone bee. More often two sets, one from each parent, are present. We shall consider the significance of this phenomenon in the next chapter. Meantime it must be borne in mind that in both sexual and asexual reproduction the

formation of the germ, whether it be product of binary fission, bud, spore, zygote, or parthenogenetic gamete, is but the beginning of the reproductive process. Further development depends upon growth, cell division, and differentiation.

Differentiation. — As to the differentiation of the new individual, controversies have been waged for generations. Aristotle long before the invention of the microscope related that the egg was structureless, and that the development of structure in that formless mass proceeded according to a definite succession of stages from the relatively few and simple structures of the early embryo to the complex organization of the adult (**epigenesis**). With the invention of the microscope, over-zealous observers and more credulous theorists came to believe that all the structures of the adult were contained either in the egg or in the sperm. This was known as the doctrine of **preformation.** In the hands of some it was developed into an elaborate theory of **encasement,** for, as they argued, if the egg contained all the structures of the adult, it must also contain the ovary and all the eggs therein. And as each such egg included the adult of the next generation and so on *ad infinitum,* the original mother of the human race must have contained the miniature representatives of the entire species, past, present, and future. Such an argument falls of its own absurdity, and the improvement of microscopes soon removed all basis for the preformation theory in its original crudity.

Internal Factors. — Development is epigenetic, and we look upon it as a series of events, in which each new change in form and function is the necessary outcome of its predecessor and the cause of its successor. The fertilized egg or the asexual spore is the protoplasmic stage on which the internal factors of heredity and factors originating in the environment play their respective parts. Embryology, as has been said, is fundamentally the study of heredity in action, but it is affected in its action by forces outside the developing cells.

Initiation of Development. — The physico-chemical mechanism by which the fertilized egg is stimulated to further development has not yet been satisfactorily demonstrated, although great progress has been made in our understanding of the process. In the light of the activation of the artificially parthenogenetic egg by physico-chemical agents and comparison with the development of naturally parthenogenetic eggs and asexual spores, it appears unnecessary to postulate anything mysterious about the phenomenon, unless complexity be a mystery.

Segregation of Organ-forming Substances. — The proof of fertilization is in cleavage, and once cleavage has taken place, the environment of each cell is modified by the presence of the other. In the development of the lancelet, *Amphioxus* (Fig. 105 *A*), the first two blastomeres give rise to the left and right halves of the body respectively. We may judge of the importance of the environment by noticing that if the egg is allowed to divide in

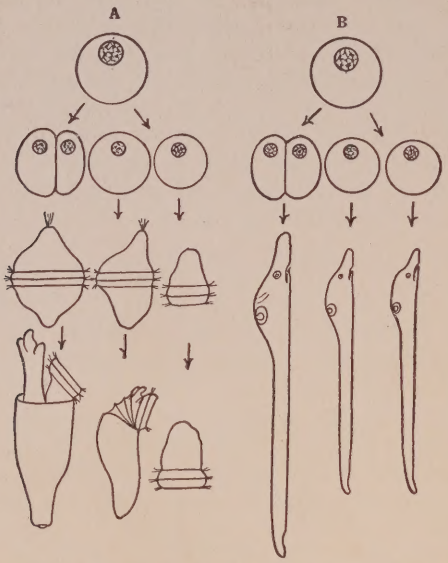

FIG. 105. — Diagrams to show the difference between determinate cleavage as shown in A, *Dentalium*, and indeterminate cleavage as seen in B, *Amphioxus*. In each case we see the type of larva which usually develops from the fertilized egg, while on the left are shown the larvae arising from each of the first two blastomeres when these are separated. (After Wilson, from Shumway.)

artificial sea-water, prepared by leaving out the calcium salts, the two blastomeres, instead of remaining attached, separate from each other. The detached blastomeres returned to normal sea-water will in many cases give rise to complete dwarf larvae (**indeterminate cleavage**) (Fig. 105 *B*).

If, however, the eggs of the mollusc *Dentalium* are treated in exactly the same manner each blastomere gives rise to only a partial embryo (**determinate cleavage**). The difference between these two types of development may be explained by the existence

of an organization in the egg. Such an organization may be seen in the tunicate *Styela* (Fig. 106), where in the fertilized egg before cleavage, at least four **organ-forming substances,** as they are called, may be recognized. Assuming that this organization comes earlier or later and that the organized matter is divided equally or unequally, the difference between the two types of cleavage may be explained.

Organizators. — In the development of the frog we have seen that the formation of the gray crescent was initiated by the

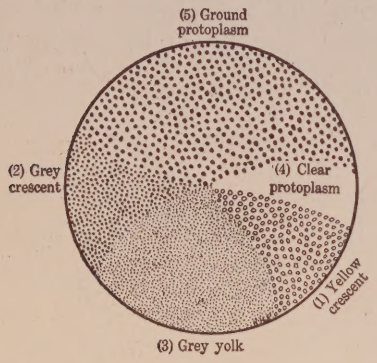

FIG. 106. — *Styela partita* (a tunicate), egg before cleavage to show organ-forming substances. These give rise to

1, larval mesoderm; 2, notochord and neural plate;
3, endoderm; 4, ectoderm;
5, the remainder of embryo.

(After Conklin, from Shumway.)

entrance of the sperm. The first cleavage usually bisects this gray crescent. Cleavage is a little more rapid in this region. Finally the dorsal lip of the blastopore, which represents a region of local overgrowth, makes its appearance here. The formation of the dorsal lip apparently organizes the blastomeres over the surface of the egg, so that even before the formation of the germ layers, the regions which will become segregated into these layers can be identified (Fig. 107). Recent experiments have shown that the removal of the dorsal lip region from one embryo and its transplantation (grafting) to another will result in the organization of a second axis of development about the transplanted sector.

The modern view of epigenesis is that each new development had some preceding **organizator,** and is itself the organizator of structures (and their accompanying functions) yet to appear. Each new structure and function alters the environment of all that has gone before.

External Factors. — The physical environment affects the developing organism directly, exactly as it does the adult, through stimulation. Mechanical, chemical, electric, photic, and thermal agents all affect development. This is directly observable in the growth of plants, where conditions of light, temperature, moisture, and soil constituents are reflected directly in the growth of the plants, not only in size but also in direction (tropisms).

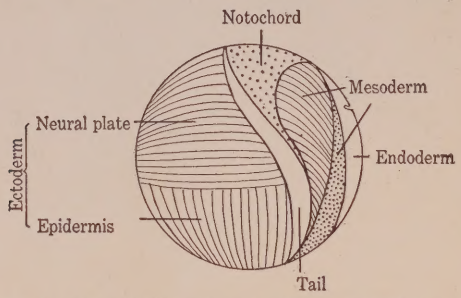

FIG. 107. — *Triton* (a salamander), embryo beginning gastrulation, to show surface areas, and the parts of the embryo to which they will give rise. The dorsal lip of the blastopore, indicated by an indentation at the right, is the organizator. (After Vogt, from Shumway.)

Temperature. — Temperature is a prime factor in the development of organisms. As we have seen in a preceding chapter, all organisms have their minimum, maximum, and optimum temperatures. The organism will develop only within a limited temperature range. Within these limits the rate of development is accelerated by increases in temperature. Excessive temperatures, but below the lethal figure, result in the appearance of monstrosities, probably because the increased temperature accelerates some chemical reactions more than others and so throws the machine out of gear.

Chemical Factors. — Water and oxygen are both important factors, owing to their presence in so many of the chemical reactions taking place in protoplasm, for the embryo is at least as metabolic as the adult. Many interesting results have been re-

corded as a result of changing the chemical constitution of the water in which aquatic eggs are developed, such as the action of the calcium-free sea-water on the *Amphioxus* and *Dentalium* eggs, or the production of cyclopean, one-eyed, minnow larvae (Fig. 108) in water to which magnesium salts have been added.

But important as are the effects of the environment, they can act only on the protoplasm of the germ, whether this be sexual or asexual. Some of the earlier steps in the development of the fertilized egg may not be affected directly by the sperm, as they are the same in the parthenogenetic egg, cleavage pattern for ex-

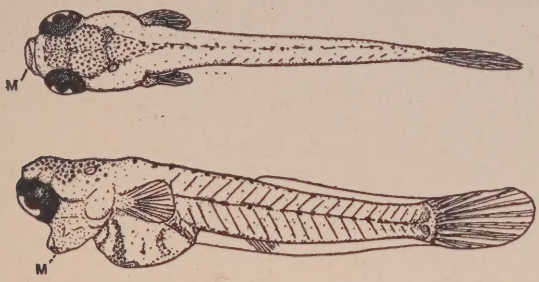

FIG. 108. — *Fundulus* (a minnow), larvae to show effect of environment on development. Above, normal larva from dorsal view; below, side view of cyclopean monster in which the eyes have fused, following development in sea-water plus magnesium salts. (After Stockard, from Curtis and Guthrie.)

ample. But sooner or later the paternal factors play their rôle in the dramatic production of the new individual. The study of the inheritance and variation of hereditary characters will form the subject of the next chapter.

Before proceeding, however, it will be well to call attention again to the fact that development is simply the organization of a new individual from a detached portion of another. In this reorganization, the metabolism and irritability of the cell are still the underlying biological phenomena. The intervention of sexual differences simply supplies a mechanism whereby a greater variety of response to a changing environment is possible, as we shall see in the following pages.

CHAPTER VII

HEREDITY AND THE GENE

It is a matter of every-day experience that the offspring resemble the parents in some respects and differ from them in others. This transmission of characteristics from parents to offspring is known as **inheritance.** The subject of the inheritance or non-inheritance of these characteristics is called **heredity,** and the biological science which deals with heredity and variation is **Genetics.**

Genetics deals with relations between the individual organisms which compose a species. The species is characterized by the resemblances between its members which seem to indicate a common origin. Yet the members show individual differences so manifold that it has been said no two organisms are absolutely identical. This variation between the members of a species is due to internal factors producing characteristics which we call **inherited** and to external factors producing characteristics which we call **acquired.**

HEREDITY

In asexual reproduction the internal factors passed from parent to offspring must be practically identical. It will be recalled that in cell division which underlies all the phenomena of asexual reproduction, the one material of the cell which is halved with meticulous accuracy is the chromatin of the nucleus arranged in chromosomes.

In sexual reproduction the variable differences existing between the parents are often mutually exclusive or **alternative.** It will be recalled also that in syngamy the zygote receives two sets of chromosomes, one from each gamete, and that some time prior to gamete formation this diploid number is reduced to the haploid number characteristic of the gamete.

The obvious method of attacking the problems of Genetics therefore is through the distribution of alternative characters in biparental inheritance, and a comparison of the statistical results with the distribution of the chromosomes in the maturation and fertilization of the gametes (reduction and syngamy).

Mendelian Inheritance. — The first clear-cut results obtained from **hybridization,** as the crossing of unlike parents is called, were those of Gregor Mendel (1822–1884), Abbot of a monastery in Brno (Brünn), Czechoslovakia. His experiments, conducted chiefly with the edible pea,[1] led him to the establishment of two laws known today as the Mendelian laws. His contributions, published in an obscure scientific journal (1866), went unnoticed until 1900 when they were discovered independently by three botanists who arrived at similar conclusions.

Free Segregation. — The great advantage in the use of the pea for these experiments lies in the fact that this species may be self-fertilized or cross-fertilized. One of the experiments performed by Mendel involved the inheritance of seed color. He used two strains of peas in one of which the seed coat of the developing embryo was yellow, while that of the other was green. On cross-fertilizing these two strains, the seeds produced, which formed the first filial generation (F_1), were all yellow, no matter from which strain he obtained the pollen. The factor responsible for the production of the yellow pigment in the seed coat is therefore said to be **dominant,** while that responsible for green is **recessive.**

When the hybrid yellow seeds of the F_1 generation were germinated they produced hybrid (F_1) plants which were self-fertilized. These plants bore both yellow and green seeds (F_2 generation) and there were three times as many yellow seeds as there were green. This is the famous Mendelian ratio (3 : 1) which always exists between the dominant and recessive characters in the F_2 generation, and is the basis for the first Mendelian Law of Free Segregation, which states that alternative characters, when brought together in hybridization, segregate freely in the second generation.

By germinating these F_2 seeds and self-fertilizing the F_2 plants which arose from them it was discovered that there were really two types of yellow seeds. The first gave rise to plants which produced as the F_3 generation yellow seeds only. Such individuals are called **homozygous** dominants. The second type developed into plants which bore as the F_3 generation both yellow and green seeds in the Mendelian ratio. Individuals of the second type are therefore like the F_1 generation and are known as **heterozygous** dominants. The green seeds of course developed into plants which produced F_3 green seeds. These three classes

[1] *Pisum sativum.*

of offspring are known as **genotypes** because they differ as to the hereditary factors which they transmit. The genotypic ratio in the F_2 generation is therefore 1 homozygous dominant to 2 heterozygous dominants and 1 homozygous recessive. Separated solely on the basis of appearance, the offspring are known as **phenotypes,** and the Mendelian ratio of three dominants to one recessive is a phenotypic ratio.

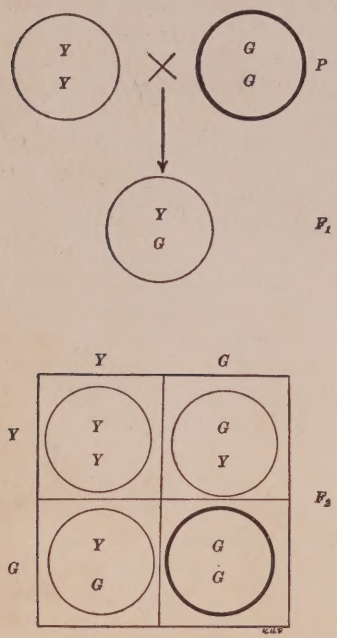

FIG. 109. — Diagram to show distribution of chromosomes bearing genes for yellow seed color (Y) and green seed color (G) in *Pisum sativum,* illustrating Mendel's first law. P, parental generation; F_1, first filial (hybrid) generation; F_2, second filial generation. The letters outside the checkerboard stand for the chromosomes of the gametes formed by the F_1 generation. (From Shumway.)

Chromosomal Behavior. — It was suggested by Sutton in 1902 that the behavior of the chromosomes in maturation and fertilization might explain Mendel's Law of Free Segregation. Let us suppose that the **gene** (as the material carrier of the factor is called) for yellow cotyledon color is located in one of the members of a synaptic pair of chromosomes while the alternative (**allelomorphic**) gene for green is located at a corresponding point in the other member of the pair. One member of the pair is paternal and the other maternal. Let us call the chromosome carrying the gene for yellow **y** and the one carrying the gene for green **g**. The zygote of the F_1 generation must have both a **y** chromosome and a **g** chromosome, the one paternal and the other maternal. It makes no difference which chromosome is paternal or maternal.

In the maturation divisions of the spore mother cells, these chromosomes unite in synapsis and form a tetrad which may be represented graphically thus: $\frac{y : g}{y : g}$. In the two divisions by which the spores are formed, each will receive one portion of the

tetrad, either **y** or **g**. The pollen tube and embryo sac formed from the microspore and megaspore, respectively, have the haploid number of chromosomes, and consequently either **y** or **g**, as do the microgametes and megagametes to which they give rise.

In the recombinations possible in fertilization, a gamete containing a **y** chromosome may unite with one containing a **y** chromosome to give a zygote with the formula **yy** (homozygous dominant) or with one containing a **g** chromosome to give a zygote with the formula **yg** (heterozygous dominant). Similarly a gamete with a **g** chromosome may unite with one containing a **y** chromosome to form a heterozygous dominant (**yg**) or with one containing a **g** chromosome to form a homozygous recessive (**gg**). The mathematical probabilities are clearly 1 : 2 : 1, the genotypic form of the Mendelian ratio.

Independent Assortment. — The second law of Mendel is that of Independent Assortment and is based on experiments involving two pairs of allelomorphic characters. One of the crosses made by Mendel was between plants originating from seed with yellow cotyledons and a round smooth seed coat, and plants originating from seed with green cotyledons and a wrinkled seed coat. The seed resulting from cross-fertilization between these parents was yellow and round. The hybrid plants arising from these seed were self-fertilized and produced four phenotypes, seed which were yellow and round, yellow and wrinkled, green and round, or green and wrinkled in the ratio of 9 : 3 : 3 : 1, all the possible recombinations. Exactly the same phenotypes in the same ratio will be obtained in the F_2 generation resulting from the cross between plants arising from yellow wrinkled seed and those from green smooth seed. This shows that the inheritance of the color is absolutely independent of the inheritance of the shape.

Chromosomal Behavior. — The explanation of independent assortment is based on the behavior of the chromosomes again, but this time we must assume that the two pairs of allelomorphic genes, **y** : **g**, and **r** : **w**, are located in two different pairs of chromosomes. The hybrid generation F_1 receives a **y** chromosome and an **r** chromosome from one parent and a **g** chromosome and a **w** chromosome from the other. In the maturation divisions of the spores, **y** and **g**, being synaptic mates, unite to form a tetrad $\frac{\mathbf{y} : \mathbf{g}}{\mathbf{y} : \mathbf{g}}$, while **r** and **w** give rise to a tetrad $\frac{\mathbf{r} : \mathbf{w}}{\mathbf{r} : \mathbf{w}}$. The two maturation divisions offer the possibility of the following haploid combina-

tions: **yr, yw, gr,** and **gw,** so that these will be found also in the gametes. The possible combinations resulting from the random fertilization of the gametes are seen in the accompanying diagram, called a Punnett square. There are in the F_2 generation sixteen combinations of gametes, forming nine genotypes, but owing to the dominance of the yellow and round genes, only four phenotypes are found in the 9 : 3 : 3 : 1 ratio.

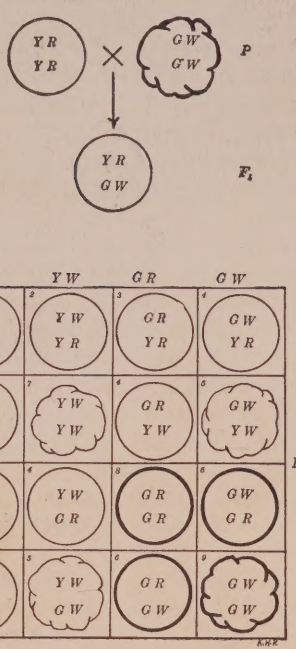

Fig. 110. — Diagram to show distribution of two pairs of chromosomes, one pair bearing genes for yellow seed color and green seed color as before, the other bearing genes for smooth seed coat (R) and wrinkled seed coat (W). This illustrates Mendel's second law. Other conventions as in Fig. 109. (From Shumway.)

If we examine the other cross, yellow-wrinkled by green-round, we find that the hybrid F_1 has exactly the same combination of chromosomes, **y, g, r,** and **w,** and therefore will have the same types of gametes, and in self-fertilization will produce the same genotypes and phenotypes according to the same ratio.

Free segregation and independent assortment can be demonstrated in experiments involving the inheritance of three or more pairs of alternative characters so long as each pair of genes is located in a different pair of chromosomes. If the number of pairs (genes or chromosomes) is represented by the symbol n, the gametes arising from the F_1 generation will fall into 2^n different classes. In the recombination of these to form the zygotes of the F_2 generation 4^n classes are possible. Owing to duplications there will be 3^n genotypes, reduced by the action of dominance to 2^n classes of phenotypes.

The Mendelian laws then may be stated as follows:

1. *The Law of Free Segregation.* — The genes preserve their

identity through successive generations uninfluenced by association with their allelomorphs.

2. *The Law of Independent Assortment.* — The genes are assorted independently in successive generations regardless of association with genes of other allelomorphic pairs.

Linkage. — Since the rediscovery of Mendel's investigations a very large amount of genetic research has been carried on in the heredity of the fruit fly[2] by Morgan and his associates. One of the principal results of these researches has been the discovery of the law of **linkage.** The phenomenon of linkage (first observed by Bateson and Punnett in 1906) is an exception to Mendel's second law, and may be illustrated by a cross between a normal fly of the wild type with gray body color and long wings to a laboratory mutant type with black body color and vestigial (short) wings. The F_1 generation has a gray body and long wings, showing that these characters are dominant. Let us now take an F_1 male and cross him with a black vestigial female. She is a double recessive, so that the phenotypes of the **back-cross** as it is called will correspond to the types of gametes produced by the male. They are black-vestigial and gray-long in equal numbers. There has been no independent assortment; black is linked to vestigial and gray to long.

If the original cross has been made between flies with gray body color and vestigial wings, and with black body color and long wings, the F_1 generation would have been gray-long as before, but on back-crossing an F_1 male to a black-vestigial female, the offspring would have been gray-vestigial and black-long in equal numbers, exactly like the parents. In this case gray and vestigial are linked as are black and long.

The phenomena of linkage are explained on the assumption that the genes for gray and black are located in the same pair of chromosomes as those for black and vestigial. Only a single pair of chromosomes is involved. The tetrad formed by the synapsis of these chromosomes would be, in the case of the F_1 generation of the first cross, $\frac{\textbf{gl} : \textbf{bv}}{\textbf{gl} : \textbf{bv}}$ and the gametes formed by the male would contain either the **gl** chromosome or the **bv** chromosome. When back-crossed to the black-vestigial female whose eggs must have the formula **bv,** the only possible phenotypes, or genotypes either, would be gray-long or black-vestigial.

[2] *Drosophila melanogaster.*

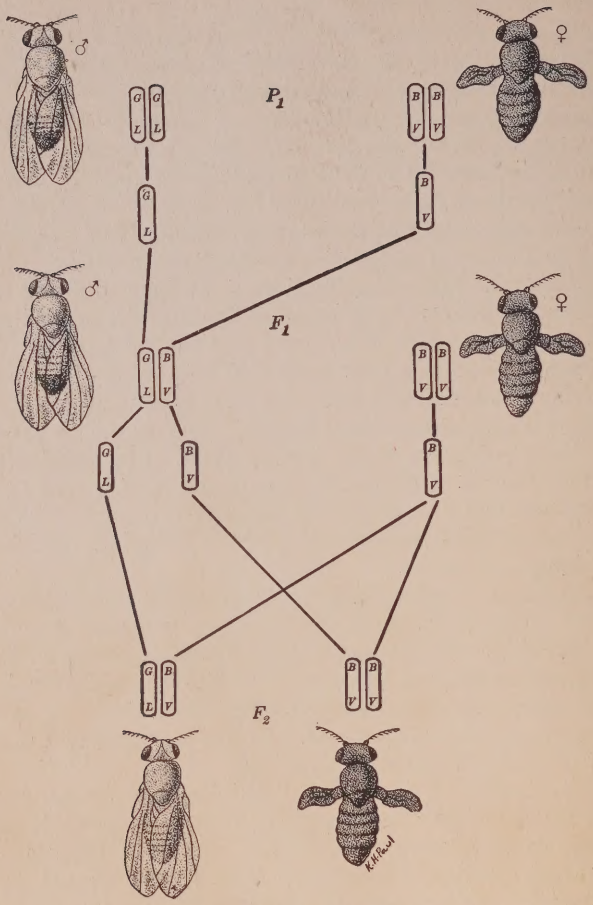

FIG. 111: — Diagram to show linkage between black body color and vestigial wings in *Drosophila melanogaster*. G, gene for gray body color; B, black; L, long wings; V, vestigial. The symbols for the genes are placed in outlines which represent the chromosomes, two in the cells of the fly, one in the gametes formed by each. Note that the F_1 male is back-crossed to a double recessive female. Their progeny are labelled F_2. (After Morgan).

In the F_1 generation resulting from the second cross, however, the tetrad would be $\frac{\mathbf{gv} : \mathbf{bl}}{\mathbf{gv} : \mathbf{bl}}$, and the sperm would contain either a **gv** chromosome or a **bl** chromosome. When back-crossed the eggs would all be of the **bv** type, so the offspring would be gray-vestigial and black-long.

In these crosses it is evident that the combinations which went into the hybrid came out unaltered, and completely linked. The Law of Linkage then may be stated as follows: the genes associated in a chromosome group tend to remain associated in succeeding generations.

Crossing-Over. — If in the preceding back-crosses, an F_1 female had been crossed to a black-vestigial male, the results would not have been the same. Taking the original cross, gray-long by black-vestigial, as our starting point, and back-crossing an F_1 gray-long female to a double recessive black-vestigial male, we find that 83 per cent of the offspring are gray-long or black-vestigial in equal proportions, while 17 per cent are either gray-vestigial or black-long in equal proportions. These two latter phenotypes are known as **cross-over** classes. The same results are obtained from the opposite cross, gray-vestigial by black-long. The F_1 gray-long female back-crossed to a double recessive black-vestigial male gives in this case 83 per cent of gray-vestigial or black-long flies in equal proportions and 17 per cent of gray-long and black-vestigial offspring equally divided. In the maturation of the egg evidently there has been an exchange of genes to give rise to new chromosome combinations responsible for the new cross-over classes.

This exchange must take place during the prophase of the first maturation division. The simplest hypothesis is that during synapsis the long-drawn-out chromosomes become attached to each other at nodes and in separating again fracture at these nodes. When the fractured portions reknit, in a certain percentage of cases, instead of uniting together, each broken fragment unites with a portion of the synaptic mate, thus effecting a transfer of chromatin material between the members of the pair. Why **crossing-over,** as this phenomenon is called, occurs in the female *Drosophila* and not in the male is still problematic.

Mapping the Chromosomes. — Through the study of crossing over and linkage relations the 400 observed allelomorphic characters of *Drosophila* have been placed in four chromosome groups, corresponding to the four chromosomes in a haploid set, which

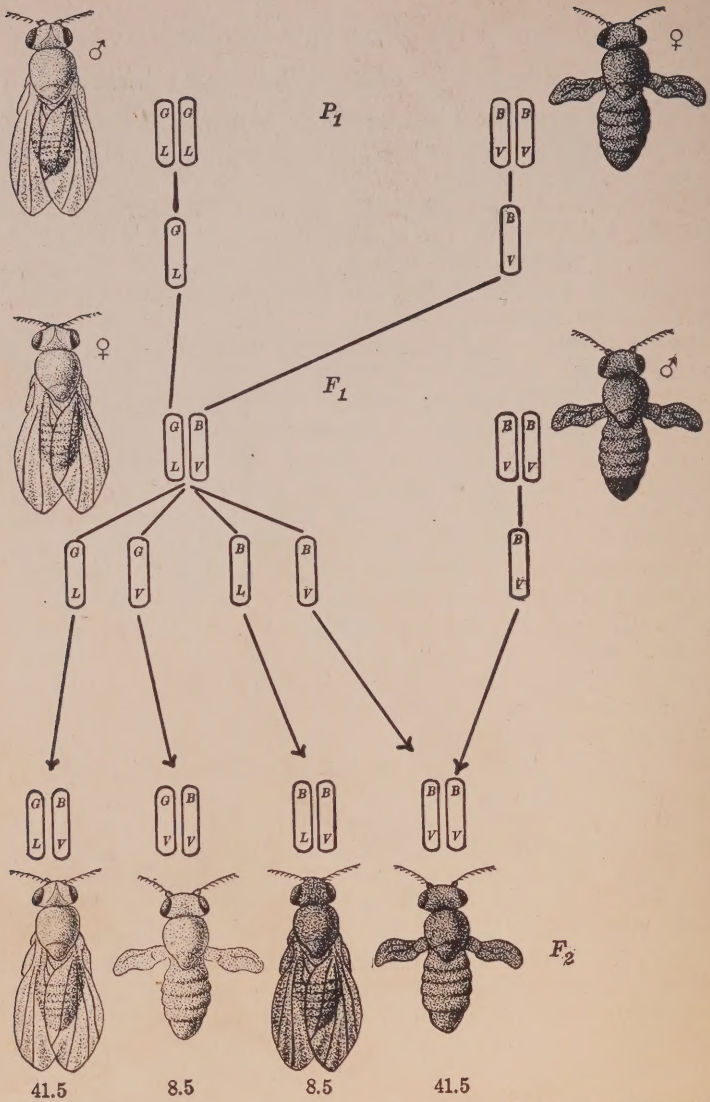

FIG. 112. — Diagram to show crossing over between black body color and vestigial wing. Conventions as in Fig. 111. Note that the F_1 female is back-crossed to a double recessive male. The figures beneath each of the F_2 phenotypes represent the percentage of the total hatch. (After Morgan.)

been numbered I, II, III, and IV, respectively. Chromosome I is a relatively short, straight chromosome; II and III are long and V-shaped; IV is small and round. In making crosses between the various combinations of genes it has been found that genes located in separate pairs of chromosomes always conform to Mendel's second law (independent assortment), whereas those located in the same chromosome pair show complete linkage in the male and crossing-over in the female.

A study of the percentage of crossing-over between different genes in the same chromosome indicates that the percentage is always a constant one for any pair of genes, e.g., $18\frac{1}{2}$ per cent for black and vestigial. This argues that the genes for black and its

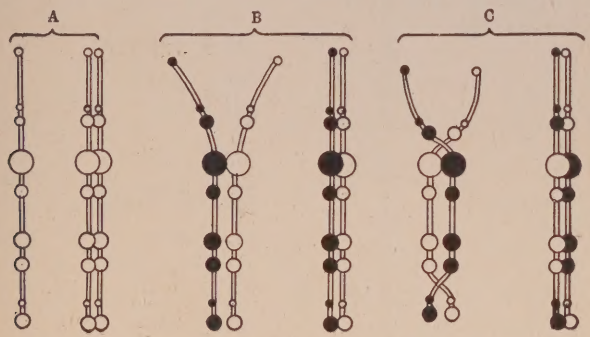

FIG. 113. — Diagrams to show behavior of chromosomes; A, splitting in prophase of ordinary mitosis; B, coming together in synapsis (first maturation division); C, exchanging material in a double cross-over. (After Wilson, from Shumway.)

allelomorph gray, and for vestigial and its allelomorph long, occupy permanent positions or loci in the chromosome. If we make the hypothesis that the percentage of crossing-over between any two such loci is a function of the distance between them in a linear series, it is possible to prepare chromosome maps, using one per cent of crossing-over as a unit of distance. The accompanying diagram shows such a map by means of which the percentage of crossing-over between any genes located in the same chromosome may be accurately predicted.

It should not be imagined that only one such fracture and rejoining takes place in a synaptic pair. As many as three nodes have been found in experiments involving the long chromosomes. The farther apart the location of the genes whose linkage relations

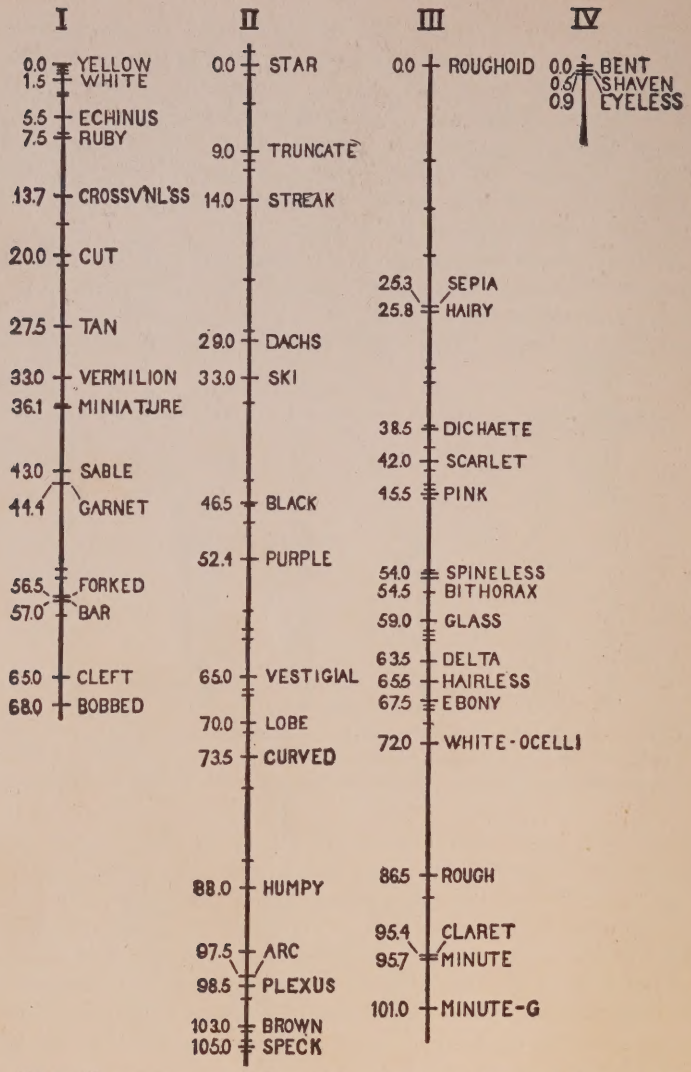

FIG. 114. — Chromosome map of *Drosophila melanogaster*, based on linkage relations. The position of the mutant genes is established by their linkage groups (I, II, III, IV) and by the percentage of crossing over between the genes within each group (arabic numerals). In group II (second chromosome) the distance between black and vestigial is 65 − 46.5 or 18.5. Compare the 17% of cross-overs seen in Fig. 112. The discrepancy is due to double crossing-over (Fig. 113, C). (After Morgan, from Newman, "General Zoölogy," The Macmillan Co.)

are to be studied, the greater is the opportunity for double or triple crossing-over. Therefore experiments must be devised to utilize only genes so near together that double crossing-over will not take place between their loci.

While crossing-over takes place only in the female of *Drosophila*, this is not true of other organisms in which linkage has been studied. In these, crossing-over may occur in either sex. As a result of this interchange of material and the consequent redistribution of the genes we must alter the law of linkage, which now takes its place with the Mendelian laws, as Morgan's law or the third law of heredity.

3. *The Law of Linkage.* The genes located in any one chromosome remain associated in succeeding generations except as they are separated in crossing-over, the frequency of which varies in direct proportion to the distance between their loci.

The Inheritance of Sex. — The chromosome which we have called I on a preceding page presents features of peculiar interest. In the female it forms a member of a pair of similar rod-like chromosomes, but in the male, while one member of the pair corresponds to this description, the other is a J-shaped body. This chromosome is known as a Y-chromosome; the others are called X-chromosomes. Because of their connection with the inheritance of sex, they are known collectively as the sex-chromosomes, to distinguish them from the other pairs, called autosomes.

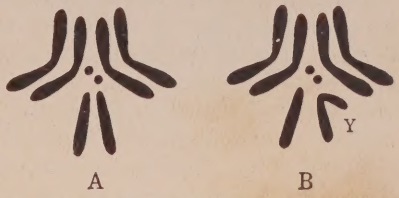

FIG. 115. — *Drosophila melanogaster*, diploid chromosome groups of A, female; B, male. The two lower chromosomes of the female are the X-chromosomes. The male has X and Y. (After Bridges.)

In the maturation of the egg the two X-chromosomes unite and form a tetrad $\frac{\mathbf{X} : \mathbf{X}}{\mathbf{X} : \mathbf{X}}$ so that the mature egg has an X-chromosome. In the maturation of the sperm, **X** and **Y** may form a tetrad $\frac{\mathbf{X} : \mathbf{Y}}{\mathbf{X} : \mathbf{Y}}$ with the result that after the two maturation divisions each sperm has either an X-chromosome or a Y-chromosome. The same distribution takes place although actual synapsis does not occur. In fertilization, the egg if fertilized by a sperm containing an X-chromosome develops into a female (**XX**),

while if fertilized by a sperm containing a **Y**-chromosome the egg gives rise to a male (**XY**). As it is the male which is heterozygous and the female homozygous, the male develops two classes of gametes and may be said to determine the sex of the offspring. More exactly, of course, as there is no selective fertilization, it is entirely a matter of mathematical probability.

Female Digamety. — It should be pointed out before going further that in birds, butterflies and some fish, the female is heterozygous and the male homozygous — a condition known as female **digamety.** In this case the sex-chromosomes of the female are called the Z-chromosome and the W-chromosome while those of the male are both Z-chromosomes. Two types of eggs are formed, but all sperm are alike so far as this pair of chromosomes is concerned.

Parthenogenesis. — The mechanism for the determination of sex in forms like some insects which have an alternation of parthenogenetic and biparental reproduction is of interest. The type of parthenogenesis in *Phylloxera*[3] is diploid, and there are two X-chromosomes in the female. In the maturation of some parthenogenetic eggs, which consists of a single equational division, one of the X-chromosomes lags behind and is not included in the nuclear membrane in the telophase. These eggs develop into males. In the maturation of the sperm, the single X-chromosome has no synaptic mate and therefore forms a dyad $\frac{\mathbf{X}}{\mathbf{X}}$ instead of a tetrad. Half the sperm receive an X-chromosome; the others have none and degenerate. The sexual eggs undergo both maturation divisions and therefore have an **X**-chromosome. When fertilized the **XX** combination is restored so that all the eggs formed by biparental reproduction become females.

Fig. 116. — *Sphaerocarpos Donnelli*, haploid chromosome groups of female and male gametophytes. (After Allen, from Sharp, "Introduction to Cytology," The McGraw-Hill Book Co.)

Sex chromosomes have also been identified in some plants, such as *Sphaerocarpos*,[4] which forms spores with a large X-chromosome or a small Y-chromosome. These develop into female and male gametophytes, respectively.

[3] *Phylloxera karyaecaulis.*

[4] *Sphaerocarpos Donnelli.*

Sex-Linked Inheritance. — Meantime let us consider the behavior of genes located in the sex-chromosomes. As the Y-chromosome is found only in the male *Drosophila*, it must either be

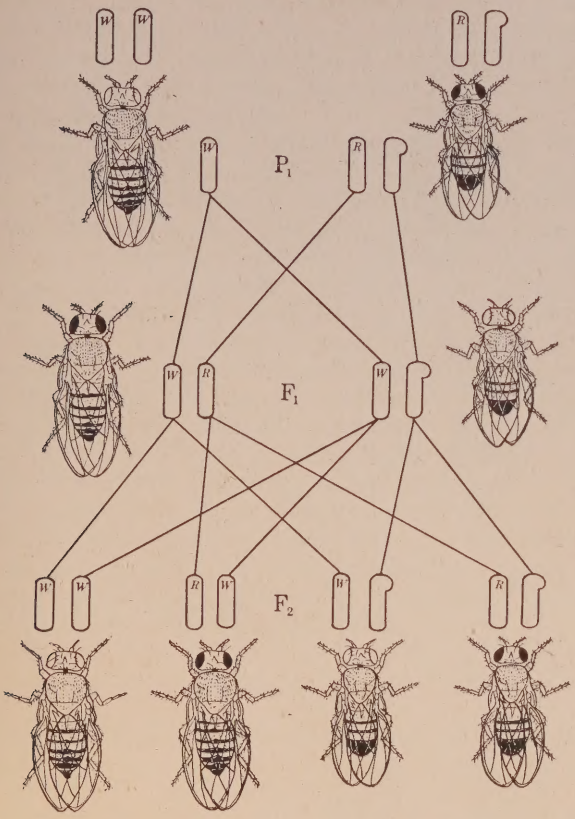

Fig. 117. — Diagram to show sex-linked inheritance in *Drosophila*, when a white-eyed female is bred to a red-eyed male. White eye-color is recessive to red. The empty J-shaped chromosome is the Y-chromosome. In the text an X-chromosome carrying the gene for white-eye color is indicated by a small x. (After Morgan.)

devoid of genes or contain only those which produce a visible effect in the development of the male. Many genes, however, are located in the X-chromosome (I), one of which is known as " white " because flies homozygous for this recessive factor have white

eyes. It is allelomorphic to red, the eye color of wild flies, as well as to several other genes at the same locus (multiple allelomorphs).

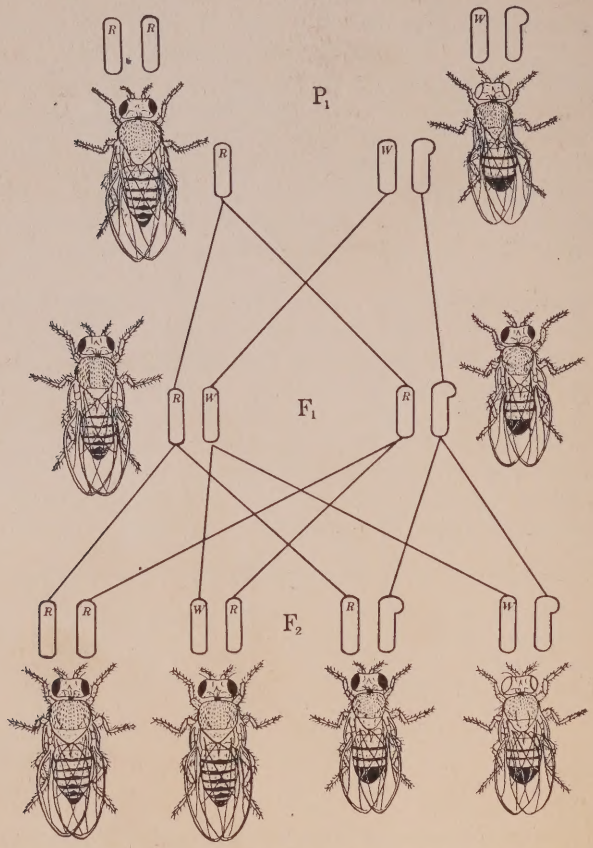

FIG. 118. — Diagram to show sex-linked inheritance in *Drosophila* when a red-eyed female is bred to a white-eyed male. Conventions the same as in Fig. 117. (After Morgan.)

If a white-eyed female, for which we may use the formula **xx,** is crossed to a red-eyed male, **XY,** the eggs will contain an **x**-chromosome, while the sperm will contain either an **X-** or a **Y**-chromosome. The F_1 generation will therefore be composed of

xX (heterozygous red-eyed) females and **xY** (white) males, for white is recessive to red. If these males and females are crossed, the female will produce two types of eggs with either an **x**- or an **X**-chromosome, while the male will produce sperm with either an **x**- or a **Y**-chromosome. The F_2 generation will therefore be made up of four classes of phenotypes, **xx** (white) females, **xX** (heterozygous red) females, **xY** (white) males and **XY** (red) males, all in equal proportions.

If on the contrary we had made the original cross between a red-eyed female (**XX**) and a white-eyed male (**xY**), the eggs would all have contained an **X**-chromosome while the sperm would have contained either an **x**- or a **Y**-chromosome. The F_1 generation therefore would have been made up of **XY** (red-eyed) males and **xX** (heterozygous red) females. If these were crossed, the females would produce two classes of eggs with either an **x**- or an **X**-chromosome, while the sperm would contain either an **X**- or a **Y**-chromosome. The F_2 generation would have four classes of genotypes, **XX, xX, XY,** and **xY,** but as the homozygous and heterozygous reds are indistinguishable there would be only three phenotypes, red-eyed females (50 percent), red-eyed males (25 per cent), and white-eyed males (25 per cent).

When crosses are made involving the presence of more than one pair of allelomorphic genes in the sex-chromosomes, the usual phenomena of linkage and crossing-over appear in the maturation of the egg. There is no crossing-over in the male *Drosophila,* as has been pointed out previously.

VARIATION

Normal Combinations. — The chromosomal mechanism of inheritance will provide for a very great amount of variation. Thus, in man, where there appear to be 24 pairs of chromosomes, the number of chromosomal combinations in the gamete is 2^{24} or 16,777,216, while the number of genotypes possible after fertilization is, in round numbers, 281,475,000,000,000. While this number is reduced in the actual number of phenotypes because of the dominance of one allelomorph to another, it will be increased enormously by the recombinations possible because of crossing-over. It has been estimated that between 2000 and 3000 genes exist in each haploid set of *Drosophila* chromosomes.

But these combinations and recombinations represent only the perpetual shiftings of perfectly definite hereditary units, the

genes, in the normal behavior of the chromosomes. We must now examine some cases of abnormalities. These are best studied in plants, because abnormal maturation divisions resulting in abnormal chromosome conditions may be perpetuated through

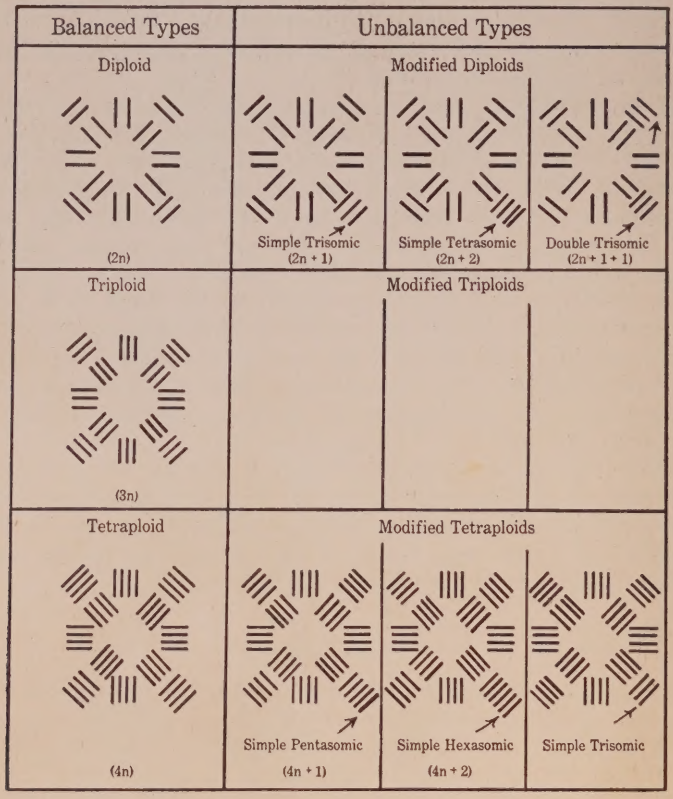

FIG. 119. — Diagram to show types of balanced and unbalanced aberrations found in *Datura*, the jimson weed. The arrows point to the extra (or region of lacking) chromosomes. (After Blakeslee.)

self-fertilization whereas, in animals, they are apt to be lost in cross-fertilization with normal individuals.

Aberrations. — In the jimson weed, *Datura*, many of the chromosomal **aberrations** have been studied by Blakeslee and his colleagues. **Balanced** aberrations are those resulting from a

suppression of cell division after the chromosomes have separated. If this occurs during or subsequent to the maturation divisions the gamete will be diploid instead of haploid. If cross-fertilization with a haploid gamete occurs, the zygote will be **triploid** ($3n$); if fertilized by another diploid gamete, the zygote will be **tetraploid** ($4n$). In this way **polyploid** types of many kinds may be built up. It has been suggested that many plant species and varieties are the result of polyploid aberrations.

Unbalanced Aberrations. — **Unbalanced** aberrations are due to the failure of one or more chromosomes to separate during a maturation division, with the result that one cell obtains $n + 1$ chromosomes and the other $n - 1$. This is known as **non-disjunction.** We have already seen in the maturation of the *Phylloxera* egg how one chromosome may be eliminated by lagging on the spindle. This also results in an $n - 1$ gamete. Such unbalanced aberrations usually have a more disturbing effect on the development of the cell. The gamete involved is often sterile or nonviable, while the zygote resulting from the union of such a gamete with the ordinary haploid type may fail to develop, or show marked somatic abnormalities. Both balanced and unbalanced aberrations take place in *Datura* (Fig. 119).

Individual chromosomes sometimes fuse with others. Or again they may fragment, and pieces may be lost, attached to other chromosomes, or even inverted and attached to the original or another chromosome upside down. The results are not always apparent in the resulting individual but are to be seen in altered linkage and crossing-over percentages.

FIG. 120.—Gynandromorph in *Drosophila melanogaster*. Note eosin eye and miniature wing on right as compared to red eye and long wing on left. This fly is male on the right side and female on the left. (After Morgan and Bridges.)

Somatic Aberrations. — Aberrant mitoses occur at other times than during maturation. Non-disjunction or elimination of chromosomes during embryonic development often results in striking differences in the regions arising from the two types of cells produced. This is particularly the case when the sex-chromosomes are involved, for one part of the body may show male characteristics, and another female, a condition known as **gynan-**

dromorphism (Fig. 120). In this particular case the fly was a hybrid with one X-chromosome containing the recessive genes for miniature wing and eosin eye color. The other X-chromosome containing the dominant genes for long wing and red eye color was lost by non-disjunction in the blastomere from which the right side of the fly developed.

Somatic aberrations are shown in particularly striking fashion by the higher plants, where all the tissue developing from one particular bud, e.g., the limb of a tree, may differ from the rest of that organism. Several horticultural varieties have arisen in this manner and have been perpetuated ever since by vegetative methods.

Germinal aberrations, however, are more apt to be submerged in the normal variation seen in maturation and fertilization.

Aberrations, whether fragmentary or total, unbalanced or balanced, not only are largely responsible for the variations existing within a given species but also serve to buttress the chromosomal theory of inheritance by supplying still another example of parallelism between the observations of breeders and the behavior of the chromosomes. In particular they support the hypothesis of the linear arrangement of the genes within the chromosome.

THE GENE

We must now inquire into the nature of the gene, how it produces its effect and whether or not it can be altered by environmental stimuli.

Nature of the Gene. — Little is known about the structure or chemical composition of the gene. It is submicroscopic, so that no direct observations can be made. Calculations made by dividing the volume of the sperm head, which is compact chromatin, by the estimated number of genes in *Drosophila*, give the figure 0.06 micron for the diameter of a gene. The microscope will not distinguish objects smaller than 0.2 micron. It must be borne in mind that the figure given above represents at best nothing more than the average amount of chromatin associated with a single gene. If the chromatin should prove to be merely a matrix for the genes, the size of these bodies would be reduced still further.

The chemical analysis of the sperm head reveals it to be composed chiefly of proteins. This class of organic compounds is

notable for the variety, complexity, and size of its molecules. The hypothesis has been offered that the gene is a protein molecule, but there is little evidence to uphold the speculation.

Activities of the Gene. — We have spoken of the genes as though each were the material agent for a single hereditary factor concerned in the production of a single unit characteristic. This, however, is not the case. The name given to each gene, e.g., " white " calls attention merely to the most striking effect produced by the presence of this particular gene when present in double dosage. A dominant gene, of course, will produce its characteristic effect when present in a single member of a synaptic pair. The double recessive white-eyed flies show also a lack of pigmentation elsewhere in the body. They are less fertile, slower in development, and generally less viable. Every gene which produces any visible effect does so by affecting various parts of the body. And of course every part of the body is affected by many different genes. In hybridization, then, numbers of genes from two different parents are combined and later segregated and reassorted in the F_2 generation. The new phenotypes are the result of the interaction, pattern, and order of the complexes of genes in each genotype formed.

Autocatalysis. — The activities of the gene take place in the cytoplasm. We may assume that the effect of the gene is primarily catalytic. It hastens chemical reactions in the cytoplasm without any loss of its own substance. Indeed, it does more: it acts as a catalyst to increase its own substance prior to each mitosis, for otherwise the chromatin would be halved at each division. Bodies of this nature are called **autocatalysts.** The genes produce their effect in the development of the gametes before fertilization, and during the development of the zygote following fertilization, and presumably throughout the life of the organism. We may form a rude sketch of the process by imagining that one gene, which we will designate as **A,** catalyzes a chemical reaction on a chemical compound **a,** which in its turn was formed during the reorganization following fertilization. As a result of this reaction a new compound, **b,** is produced. Gene **A** has no effect on compound **b,** but another gene, **B,** acts as a catalyst to produce among others a compound **c.** This is not affected by **A** or **B** but is catalyzed by **C,** producing a compound **d.** So the series continues. Meantime the fertilized egg divides, and compound **d** is either divided equally between the two blastomeres or unequally up to the point where one

blastomere has all of this compound and the other none. The reactions which make up the metabolism of these two blastomeres would be alike in the first case (determinate cleavage), unlike in the second (indeterminate cleavage). And the subsequent activities of the genes in indeterminate cleavage will differ because of the different materials present in the different blastomeres, as well as the different forces brought to bear from the environment.

Mutation. — The three laws of heredity dealing with segregation, assortment, and linkage are founded on the individuality and persistence of the genes. But the very fact that **alternative** characters depend on the presence or absence of allelomorphic genes at particular loci in the chromosomes argues that one of the genes is a derivative (**mutant**) of the other.

The intensive study of genetics in *Drosophila* by Morgan and his students has resulted in the identification of nearly four hundred different genes, the loci of which have been determined by linkage and cross-over studies. The new classes of flies which have appeared in the laboratory are known as mutants, and the assumption is made that they are due to changes in the genes which are responsible for the allelomorphic characteristics in the fly from which the mutant arose. Inasmuch as the new mutants breed true and hybridize with the original stock according to the three laws of heredity, the change may be said to result in the production of a new gene, at the same locus in the chromosome as the original one. Thus the gene for white eye-color arose in a stock of red-eyed flies and is derived from the gene for the latter characteristic. The gene for vestigial wings arose from that for long wings. The gene for black body-color comes from that for gray body-color, and so on.

Multiple Allelomorphs. — The genes at some loci seem more susceptible to changes than those in other regions of the chromosome. Thus the gene for red eye-color in chromosome I has given rise to eleven different (multiple) allelomorphs. These in turn may give rise by mutation to some of the other mutants, including the original allelomorph red.

Somatic Mutations. — Mutations may occur in both germ cells and soma cells, and apparently at any time in the life of the cells. Somatic mutations can be transmitted only through asexual reproduction, as in plants. But somatic mutations may be accompanied by corresponding changes in the germ cells, so that characters appearing during the life of an individual may also

appear in the offspring. Supposing a new gene which is dominant to the normal allelomorph to arise in one chromosome prior to the segregation of the germ and soma cells. This would manifest its result during the life of the organism and would be transmitted in inheritance. (See page 214.) The appearance of a recessive gene would show no phenotypic results in the individual concerned nor in any of the offspring, unless through inbreeding or self-fertilization homozygous recessive genotypes should be formed.

Dominant and Lethal Mutations. — All mutations in genes produce changes in the metabolism of the cells. If these are very great the genes are said to be dominant, as the presence of such a gene in a single chromosome will cause visible phenotypic changes. If the changes are not so great but the presence of the gene in each member of a synaptic pair produces visible results, the gene is said to be recessive. Even slighter changes are caused by mutant genes whose only effect consists in augmenting or diminishing the effects of others. These must be studied by special methods which cannot be considered here. All mutations produce non-adaptive changes which may even cause death and are therefore known as lethal mutations, dominant if lethal in single dosage, recessive if the gene must be present in both chromosomes to cause death. The presence of lethal genes is recognized by disturbances in the phenotypic ratios.

Rate of Mutation. — The rate of mutation, or more properly the number of mutations which have been recorded, is small. In *Drosophila* where 400 visible mutations have been recorded and over 20,000,000 flies examined, about one in 50,000 is a mutant. Invisible and lethal mutations arise in greater numbers. The percentage of mutations is increased by increases in temperature. Flies bred at a temperature 10° C. above normal room temperature had approximately three times as many mutations as the controls. Very recently treatment by X-rays and radium has been successful in stepping up the frequency of mutation. Irradiated flies produced approximately 150 times as many mutations as the controls.

From these experiments the conclusion has been drawn that a mutant gene is the result of a change in the chemical constitution of the original gene, thus altering its catalytic effect. Once altered, the mutant gene acts as an autocatalyst, persists through generations, maintaining its individuality, and reproducing itself as a separate entity until a new mutation changes it again.

The Gene Theory. — The study of Genetics then carries our conception of the cell as the unit of the organism still further, and makes the gene the physiological unit of the cell. These entities, invisible though they are, have been located in the chromosomes. They are distributed from cell to cell according to the mechanism of chromosome division in mitosis. In maturation and fertilization they segregate and are assorted according to the reduction of the chromosomes in the maturation divisions characteristic of sexual reproduction. They act as autocatalysts, reproducing themselves, and accelerating the various chemical reactions of metabolism. Changes in genes produced by mutation result in changes in cell-metabolism and irritability reflected in structural and functional changes in the organism.

The importance of this conception of the gene in modern Biology cannot be overemphasized, and the theory of the gene may be said to occupy the same position today as the cell theory held in the Biology of the last generation. It provides a unifying idea which has proved most helpful in understanding the problems not only of inheritance and development but of variation as well. If the cell is the architectural unit of the organism, the gene is the biological element beyond which biological investigation has not been able to advance. Entirely hypothetical in that its existence is demonstrated by mathematical analysis rather than by microscopic observation or microchemical tests, it has been the basis for innumerable experiments, and has inspired new methods of approach to traditional problems. Theoretically it should prove the connecting link between the biological concepts of the species and organism and the physico-chemical concepts of matter and force.

CHAPTER VIII

ECOLOGY AND THE COMMUNITY

Each new organism commences its development equipped with a complete set of genes (two sets in biparental inheritance). But from the moment of its origin it is exposed to the play of forces outside its own body. As we have noted, in some instances these affect the genes directly and cause them to mutate (**germinal** effects). More often these external forces modify the action of the genes, rather than the genes themselves, which remain unaltered. Such effects are called **somatic.** Germinal changes result in somatic effects often of great extent; there is no evidence, however, that somatic changes induce mutations of the genes. We have already seen how the organism, by virtue of the irritability of its cells, responds to environmental changes at all times during its life. The responses by means of which the organism continues its existence otherwise unaltered we have called adaptive, and the structures by means of which the organism makes adaptive responses are known as adaptations.

We must now examine the relationships existing between organisms and that part of the universe outside them but affecting their existence directly or indirectly, i.e., the **environment.** The study of organisms in relation to their environment is called **Ecology.** There are two methods of attack.

The first considers the organisms of any particular species as affected by all the factors of the environment, including their relations to the other plants and animals by which they are surrounded. The emphasis is on the single organism (or species). Ecology of this kind has been called **autecology** and resembles closely that sort of study for which the words " natural history " or " biology " are often used, as when one says " the natural history of the frog " or " the biology of wheat."

Synecology. — The modern point of view as stated by Shelford is that " ecology considers not only the relations between organisms in a community made up of different species, but also the relations of each species to its environment as a whole and to each of the conditions which make up the environment." This

type of ecology may be called **synecology,** for the emphasis is on the community. The relationship between ecology and the other biological sciences which we have had occasion to examine in preceding chapters corresponds closely to the relationships between human anatomy, physiology, etc., which are concerned with the human individual, and sociology which deals with the human community.

THE COMMUNITY

What then is a community? It is an assemblage of plants and animals occupying a common habitat or area with similar **climatic** conditions. The plants and animals existing under similar general (climatic) conditions make up what is called a **formation,** for example, a desert formation; while the local (**edaphic**) conditions may result in the existence of what is termed an **associes** within the formation, e.g., a stream community in a desert area. The community is not to be thought of as static. As set forth by Warming in 1909, the community grows, develops, invades new territory, competes with other communities, retreats, and dies. In its growth it shows seasonal rhythms, annual cycles, and periodic changes often extending over even longer periods.

The Ecological Method. — This dynamic conception of the community rests upon series of accurate ecological surveys, which are more in the nature of a census showing the numbers of individuals belonging to each plant and animal species, than like the older check-lists which merely assembled the names of the species observed. The species most conspicuous themselves in point of numbers, or most conspicuous in influence are known as **predominants.** These are graded into different classes according to their relative influence in the community.

Climatic Factors. — An analysis of the factors affecting the origin and development of the community shows that these fall into three classes: (1) the general conditions of temperature, moisture, barometric pressure, light, soil conditions, etc., which we know as climate; (2) the local conditions, principally those of moisture, soil conditions, and light, which may cause breaks or wounds in the major habitats or formations; and (3) the biotic relationships existing between the predominants and other species of the community.

Temperature. — We have already had occasion to refer to the effect of temperature upon the metabolism and therefore

the irritability and development of the cell. It must also have a preponderant influence upon the activities of the organism and in determining the maintenance and reproduction of the species in any given habitat. This is recognized in our common denomination of climates as frigid, temperate, and torrid. It is a matter of common knowledge that the plants and animals found in these climates differ widely from each other.

In temperate climates also there are seasonal changes of temperature, not only in the course of the year (spring, summer, autumn, and winter) but also during the day. With these are associated other changes such as those of moisture and light. It is therefore common to find within any developed community (**association**) seasonal societies, the taxonomic composition of which varies according to the time of year. This is demonstrable in the life of the community and in censuses taken at different hours and seasons.

Moisture. — Moisture affects the activities of both plants and animals. The sources of moisture are (1) humidity or water in the atmosphere, (2) soil water, and (3) rain either during rainfall or after its collection as surface water, but before its disappearance through evaporation (by which it is added to the atmospheric water) or through absorption (by which it is added to the soil water). We have already observed the dependence of the plant upon soil moisture for continued existence and growth and the effect of humidity upon the rate of transpiration. The animal too requires water, which is absorbed through the skin or taken in drinking. In nature, temperature and humidity vary together in an approximately reciprocal relationship.

Barometric Pressure. — The effects of barometric pressure upon animals are direct. Increases in barometric pressure increase the general rate of metabolism; a falling barometer lowers the general rate. Air currents affect the distribution of plants, the amount of transpiration, and the distribution of small animals such as insects. The rate of transpiration in plants and of evaporation in animals is the combined effect therefore of atmospheric temperature, humidity, barometric pressure, and air currents, upon the amount of water available for such losses.

Light. — The total amount of light, the quality of the light in terms of wave lengths present, the direction of the light rays, and the daily march of the intensity affect the life of plants directly through photosynthesis. Animals are affected indirectly in that the amount and quality of their food, derived from the plants, is

dependent upon the conditions of light. This affects their growth and activity. To some extent the light also affects their ability to obtain food according to their power of vision. Thus the owl, a successful hunter at night, may be so defenseless during the day that he flees before the clamoring attacks of crows.

Light effects are modified by other climatic factors, such as cloudiness, water vapor, etc., which vary seasonally with temperature, moisture, barometric pressure, and air currents. It is also influenced by biotic conditions, principally by the shade of the vegetation. It has been shown, for example, that the forest crown is selective as to the wave lengths absorbed and transmitted because of the chlorophyll present. The amount of transmitted light of course decreases from the crown towards the forest floor.

Climatic Types. — It is evident that the community is in a state of continuous change in so far as the individuals concerned vary their activities with the varying climatic factors mentioned above. Yet regions with similar climatic conditions show similar types of communities the world over. The individual species may differ in different parts of the earth's surface, but plants and animals with adaptations of the same general type will always be found present under similar climatic conditions.

Local Conditions. — We have already referred to the fact that in a great formation, such as a desert, there may be ecological gaps or breaks due to local conditions of moisture and soil condition, such as the existence of an oasis. Here will be found an associes of plants and animals entirely different from those to be seen in the desert proper.

Very often such local conditions may result in the temporary appearance of a community covering a very small area of **microhabitat.** Thus the death of a large animal on the prairie will create local conditions favoring the multiplication of many small scavengers, principally insects and worms, and particularly bacteria. These predominants often destroy their habitat by their own activities.

So too in aquatic communities, local conditions such as the existence of a rocky promontory extending into a beach which is otherwise a sandflat, will cause the creation of an associes of animals quite different from those inhabiting the sands.

These ecological islands often represent developmental stages in the life of the community, for the causes of the local conditions may be entirely temporary, and with their disappearance the

associes is swallowed up into the larger community by which it is surrounded.

Biotic Relationships. — Climatic conditions, except for seasonal variations, are relatively permanent; edaphic conditions may be relatively temporary; but the development of the community depends upon the relationships between the plants and animals of which it is, from time to time, composed.

These relationships have to do with food or protection. Plants compete with each other for moisture and light. Animals compete with each other for food which they may derive directly from plants (herbivores) or from the bodies of other animals (carnivores). The trees supply not only food but protection for many of the smaller forms of animal life, and their shade is an important factor in the development of many smaller plants.

Intra-Specific Relationships. — The relationships among plants of the same species are seldom close, and result only from the fact that plants being relatively immovable tend to remain in the region where they developed. Sometimes a common stock remains in physical connection, such as the great mangrove colonies, but this is as far as the plant society develops.

Among animals, however, we find societies ranging from loosely knit aggregates, such as the schools of menhaden which are found off the Atlantic coast, and the herds of bison which once swept the Western prairie, to the highly organized societies of the bee and the ant. In these forms in which behavior is supposed to be entirely instinctive, we find the most elaborate specialization of labor among the different castes, communism to the *n*th degree, agriculture, animal breeding, architectural engineering, slavery, and war.

Inter-Specific Relationships. — Close interrelationships among members of different species form an intergrading series commencing with the relationship between the **predator** and his prey, between the **parasite** and his host, between **commensals** who use the same food to the disadvantage of neither, and finally between **symbionts,** whose association is advantageous to both.

The predator devours its prey entire, or at least generally kills its prey before or during the consumption of its food. The parasite, however, obtains its food from the living body of the host. Plants are parasitic on plants and on animals; animals are parasitic on animals and on plants.

Plant Parasites. — Nearly all the plant parasites are included among the fungi (Chapter X). Here belong the bacteria, many

of which are free-living saprophytes. Others are found within the tissues of other plants and animals. Some cause disease and death (**pathogenic** bacteria); others are merely commensals, using partially digested foodstuffs. Some may actually be symbionts, such as the forms normally found in the mammalian large intestine, which break down cellulose. The molds are saprophytes or are parasitic on other plants and animals. Thus *Saprolegnia* (Figs. 158, 159), the water mold, is usually found on the bodies of dead animals but sometimes attacks living animals, particularly on cuts or abrasions. Many plant diseases are caused by the mildews and rusts in this group. Some human skin diseases, e.g. ringworm, are caused by molds. Some few of the flowering plants, like the dodder and mistletoe, are parasitic.

Animal Parasites. — Animal parasites are divided into two groups: **ectoparasites,** which are found on or immediately below the surface of the host, and **endoparasites.**

Ectoparasites. — Ectoparasites are distinguished from predators only by their smaller size. Some ectoparasites are free to move over the body of the host and from host to host, like the parasitic insects, the flea and the louse. Others are attached, like

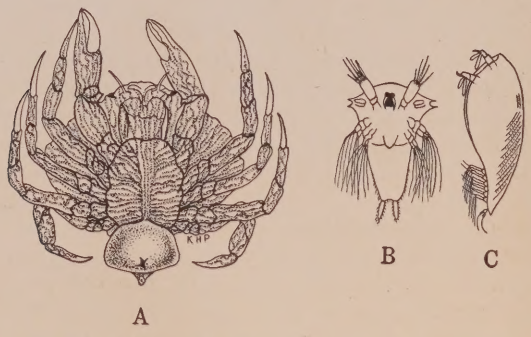

Fig. 121. — *Sacculina*, a parasitic crustacean. A, a crab parasitized by *Sacculina*. The stipple represents processes of the parasite extending into the body of the host; B, C, larval stages of *Sacculina*. Compare Fig. 131. (After Doflein.)

certain parasitic entomostraca, which have lost many of their ancestral characteristics. Most remarkable of all these is a form known as *Sacculina* (Fig. 121), whose larva is undoubtedly that of a crustacean, but which settles down on the abdomen of a crab and grows long processes into the body of the host. These

absorb nutriment directly from the crab's tissues. Meantime the *Sacculina* waxes larger but loses all its appendages, sense organs, even its digestive tube, and becomes practically nothing but an enlarged reproductive system — an egg bag, curiously reminiscent of Nietzsche's " reversed cripple." The effects on the host are various: sometimes the sex-glands are destroyed and the external secondary sexual characters reversed.

Endoparasites. — Endoparasites particularly noteworthy are protozoa of many kinds, perhaps the best-known being the malaria organism which manifests the interesting phenomenon of an alternation of generations in two successive host species. This organism[1] (Fig. 122) reproduces asexually in the blood of man, sexually in the intestine of the mosquito, by which it is transmitted from one human to another. Many worms are entirely parasitic. Some of these will receive mention in Chapter XI.

Commensals. — It is difficult to distinguish between parasite and commensal, particularly in cases where the doubtful species inhabits the digestive tube of the host. Often the suspected parasite is merely living within the tube and enjoying a saprozoic existence, deriving its food from the digested nutriment of the host before this is absorbed.

Symbiosis. — There are several examples of symbiosis between plant and plant, animal and animal, and plant and animal. Thus the lichens (Fig. 161) found on the bark of trees and exposed rocks are made up of two types of plants. The greater part of the mass is made up of a fungus. In this are found the cells of one of the algae. The fungus absorbs water and mineral salts from bark or rock. The algal cells obtain these from the fungal cells and absorb carbon dioxide, which by means of their chlorophyll they build up into sugars which the fungal part of the lichen absorbs. This association is beneficial to both, and the association of the two plants produces a plant body which is different from either and from other lichens, so that botanists treat the complex as a plant species.

The ant-aphid assembly (Fig. 123) is an interesting one. The aphids which live on corn roots are cared for during the winter by the ants and by them transported back to the roots of the freshly planted corn. The advantage to the ants is the secretion by these " ant cows " of a honey-like substance which the ants apparently utilize as food.

[1] *Plasmodium malariae.*

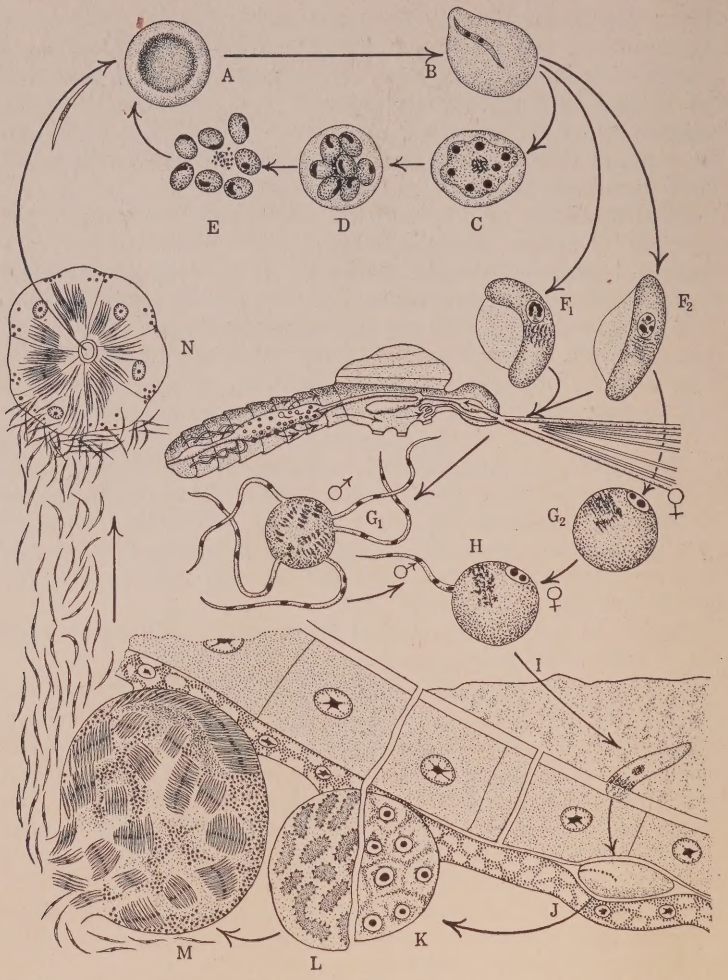

FIG. 122. — Life history of *Plasmodium*, a protozoön parasite, the causative agent of malaria. A, human red blood corpuscle; B, same parasitized by sporozoite stage; C–D, spore formation; E, release of spores into blood plasma (all in human blood stream). F_1, G_1, development of microgametes; F_2, G_2, development of megagamete; H, syngamy (all in mosquito intestine). I–J, zygote penetrating wall of intestine; K–M, encystment and spore formation (in wall of intestine). N, escape of spores to salivary gland of mosquito. (Combined after several authors.)

The green *Hydra* contains in its endodermal cells minute green algae which synthesize their food from carbon dioxide and water excreted by *Hydra* and give off oxygen which can be utilized by *Hydra*.

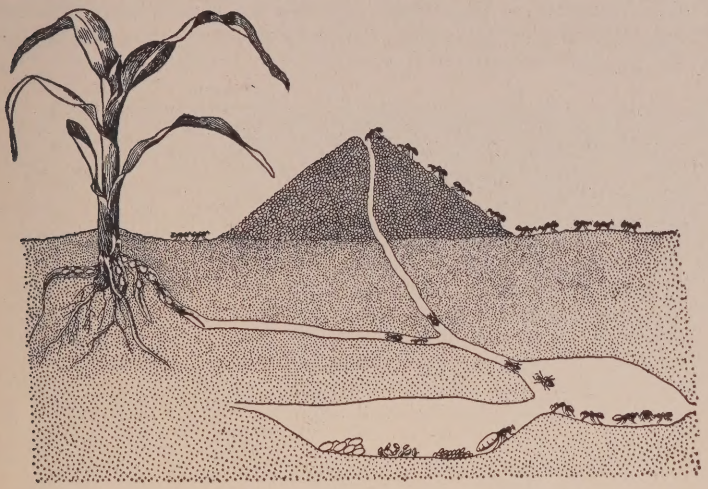

FIG. 123. — Diagram to show ant-aphid assembly. See text for description. (From Curtis and Guthrie.)

Enough has been said to show that the relationships between the different organisms of the community play as important a part in the development of the community as the climatic and edaphic factors. Further examples will be mentioned in the following pages.

TYPES OF COMMUNITIES

The physical factors determining the climatic, edaphic, and biotic conditions of terrestrial, aquatic, and marine communities are so diverse that it seems advisable to examine these separately.

Terrestrial. — The land community is described in terms of its vegetation landscape rather than in terms of its flora. A forest, a swamp, a desert, etc., are general terms which carry with them a meaning regardless of the species of which they are composed. A coniferous forest is composed of evergreens, regardless of species, whereas a deciduous forest is made up of hardwoods, whether in

North America or Europe. The dominant species in a community are usually the trees, which because of their size, their shade, their own food requirements, and the shelter and food they afford other organisms are the most important and conspicuous members of the community. Also they exercise an important influence throughout the entire year. Slow to develop, they extend the

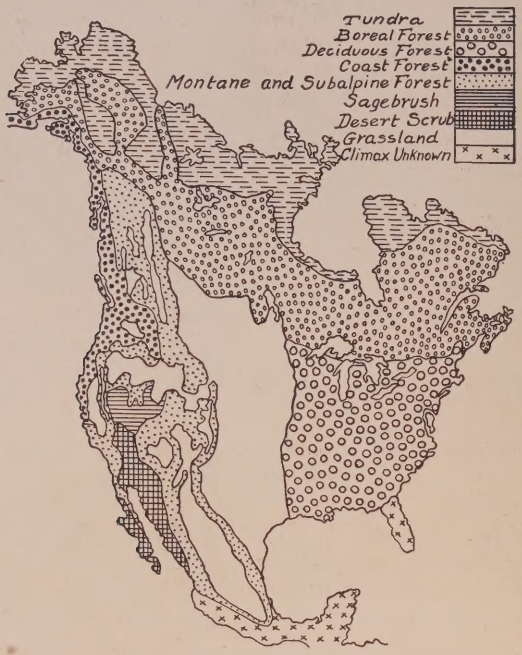

Fig. 124. — Map of North America to show major vegetation areas. (After Weaver and Clements, with modifications by Shelford.)

boundaries of the community very gradually, but resist changes in climatic and biotic conditions with equal firmness. The less important shrubs, grasses, etc., which are present and exert a smaller but still measurable effect on the composition of the community are called **influents.**

Vegetation Areas. — The general types of vegetation areas are (1) the forest, (2) the grasslands, (3) the desert, and (4) the tundra. The map (Fig. 124) shows the distribution of these vegetation areas in North America.

The Forest. — The forest is characterized by the presence of continuous stands of trees and includes (*a*) tropical rain forests, which are continuously moist and warm and are exposed to intense light with the result that the broad thin leaves are not shed periodically; (*b*) deciduous forests, which are periodically dry or cold; (*c*) coniferous forests with evergreens whose narrow thick leaves withstand more irregular periodicities such as winter

Fig. 125. — Illinois forest. (Photograph by V. E. Shelford.)

rains, prolonged dry seasons, etc.; and (*d*) winter rain forests, such as the semi-desert of California, characterized by trees and shrubs with broad thick leaves, often evergreen hardwoods.

The Grasslands. — The grasslands include all those great stretches in which the grasses are the dominant type of vegetation, and trees occur in small stands where conditions are favorable, chiefly along water courses. Typical grasslands are (*a*) the tropical **savanna,** which represents a transition between the tropical forest and the **prairie,** extending from the forest margin with individual groves and thickets of trees and brush; (*b*) the tropical prairie (or **steppe**) which is a great area of grasses adapted

to continuous warmth but long dry seasons. The temperate savanna (*c*) intergrades from any of the temperate forests mentioned in the preceding paragraph into (*d*) the temperate prairie, characterized by extreme summers and winters, slight rainfall, and strong winds.

The Desert. — The desert is characterized by a warm, dry climate. The principal vegetation consists of scrub brush and

Fig. 126. — Illinois prairie. (Photograph by V. E. Shelford.)

bunch grass, although during the short rainy season there are rich displays of flowers. The cactus is a type of plant in the North American desert which stores water and thus affects the ecological balance of the community. The desert intergrades with both the prairie on the one hand and the evergreen forest on the other. The belt between is called the **chaparral** and has hot dry summers and milder rainy winters. The plants have relatively small thick and shiny leaves.

The Tundra. — The **tundra,** on the contrary, is characterized by long cold winters and little rainfall. In these so-called barren lands, the ground often thaws only at the surface, and large

areas are covered with snow perpetually. There are dense growths of grass and miniature shrubs; herbaceous plants are found during the summer, and swamps and ponds abound.

Plant Components of the Community. — The relationship between the dominant plants of the community and the influents is primarily one of food supply, and to a slighter extent that of protection. The various levels of ground moisture are tapped by the roots of the different adaptation types of plant life present, so that there is a direct competition for the water and inorganic salts of the soil. The growing roots send out fresh advance guards of root hairs which take up water and salts and leave behind excreted wastes at progressively lower levels. Similarly the growing shoots of the dominant trees have the first chance at the undiluted rays of sunlight, while every other plant beneath the forest crown obtains its solar energy more or less diluted, according to its height above the forest floor.

Bacteria. — But it must not be forgotten that there are other less highly organized plants than the spermatophytes (seed plants). Mosses, lichens, and fungi grow in sheltered spots between or even on the more dominant types. Holophytic and saprophytic unicellulars exist in large numbers. Particular attention must be paid to the activities of the bacteria and other fungi in breaking down the proteins, carbohydrates, and fats of plant and animal bodies, known in general as fermentation. The fermentation of proteins in the presence of oxygen is generally not attended with offensive odors (decay); in the absence of oxygen, however, anaërobic bacteria cause putrefaction. Both processes are catalyzed by enzymes secreted by bacteria which utilize the energy obtained in lieu of sunlight for the endothermic reactions by which they build up the carbohydrates, fats, and proteins of their own protoplasm. There are few bacteria but a number of other fungi (molds, etc.) which are able to decompose fats by similar processes and with the same results, obtaining energy for the constructive reactions of the fungi themselves. An example of carbohydrate decomposition is alcoholic fermentation, which goes through two stages. The first is carried on by the yeasts, which contain an enzyme known as **zymase.** This catalyzes the exothermic reaction in which glucose is broken down into ethyl alcohol and carbon dioxide. The sugar is absorbed by the yeast, acted on by the intracellular zymase and secreted again as alcohol and carbon dioxide. The oxidation of alcohol to form acetic acid and water is due to the activities of the acetic

acid bacteria, which utilize the alcohol as a food and the energy released in its decomposition for constructive processes.

Nitrogen Fixation. — The nitrogen which the plant uses in building up its proteins is obtained from the soil in the form of nitrates. These are built up by the so-called nitrogen-fixing bacteria.[2] These forms oxidize organic compounds in the soil and so secure the energy by means of which they build up nitrogen-containing organic compounds in their own bodies. When they die these compounds are broken down to form nitrates which can be utilized by the green plants. The ammonium salts resulting from the decomposition of plant and animal bodies are transformed into nitrites through the activities of bacteria belonging to the genus *Nitrosomonas*, and the nitrites are converted into nitrates by several species of *Nitrobacter* which are always found with *Nitrosomonas*. Both these reactions are oxidations, liberating energy which can be utilized by the bacteria in the endothermic processes through which they build up the components of their own protoplasm. All these activities through which the colorless (non-chlorophyll-containing) plants build up organic compounds are known collectively as **chemosynthesis.**

Still other bacteria carry on the reverse processes, i.e., the conversion of nitrates into nitrites, oxides of nitrogen and free nitrogen, thereby removing nitrogen from the soil and impoverishing it. These bacteria are known as denitrifying bacteria.

Carbon and Nitrogen Cycles. — The activities of these chemosynthetic plants together with those of the photosynthetic, holophytic plants result in the building up of carbon and nitrogen atoms into organic compounds which can be utilized by the holozoic animals, or which decay and are fermented by bacterial action. The animal body breaks down these compounds and liberates ammonium salts, water, and carbon dioxide. The animal body may be utilized as food by other animals, thus prolonging the cycle, or it may be decomposed after death by the putrefactive bacteria. The accompanying diagrams illustrate the cyclic changes possible for carbon and nitrogen atoms.

Animal Components of the Community. — The most important animals of the community sometimes act as **dominants.** Thus the bison was probably the means of keeping the great plains of the West in a short grass condition prior to the coming of the white race. More often they are termed **influents** in that they have exercised sufficient effect upon the activities of other animals

[2] *Clostridium pasteurianum* and various species of *Azotobacter.*

to hold them in check or encourage their multiplication. Thus wolves may hold larger herbivores in check. Or their influence may be sufficient to affect the plant life, e.g., the actions of

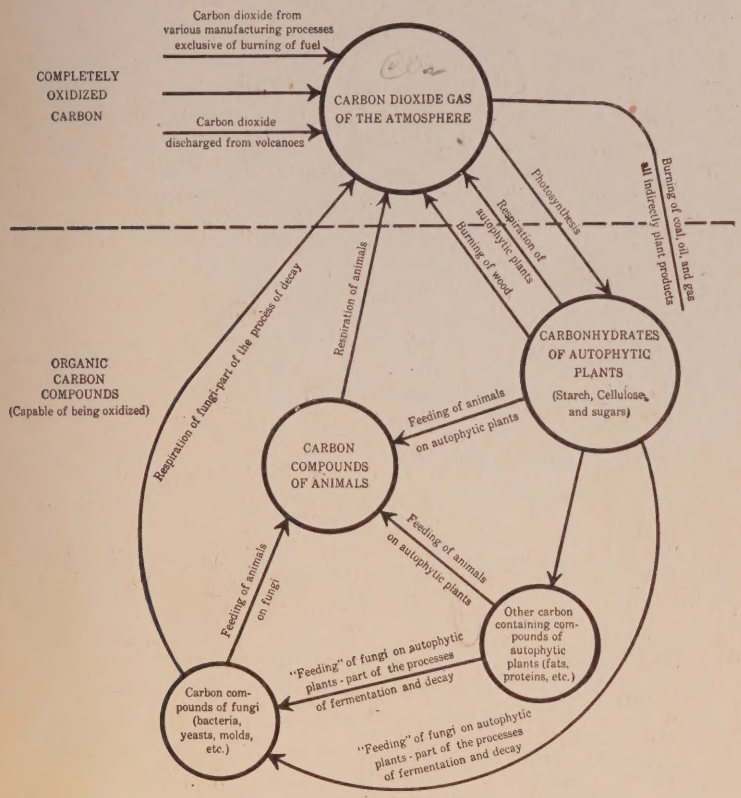

FIG. 127. — Diagram to show carbon cycle with particular reference to the occurrence of this element in the bodies of plants and animals. (From Holman and Robbins.)

rodents in opening up sod will help the forest to encroach upon the prairie.

Subdominants and **subinfluents** are forms which appear in the community or exercise their influence for only a portion of the year, such as insects and migratory birds. The influence of insects in cross-pollinating flowers has already been mentioned.

Animals of the Forest. — In a forest community, we find in the substratum worms which feed upon partially decomposed vegetable material in the soil, or coming to the surface at night devour

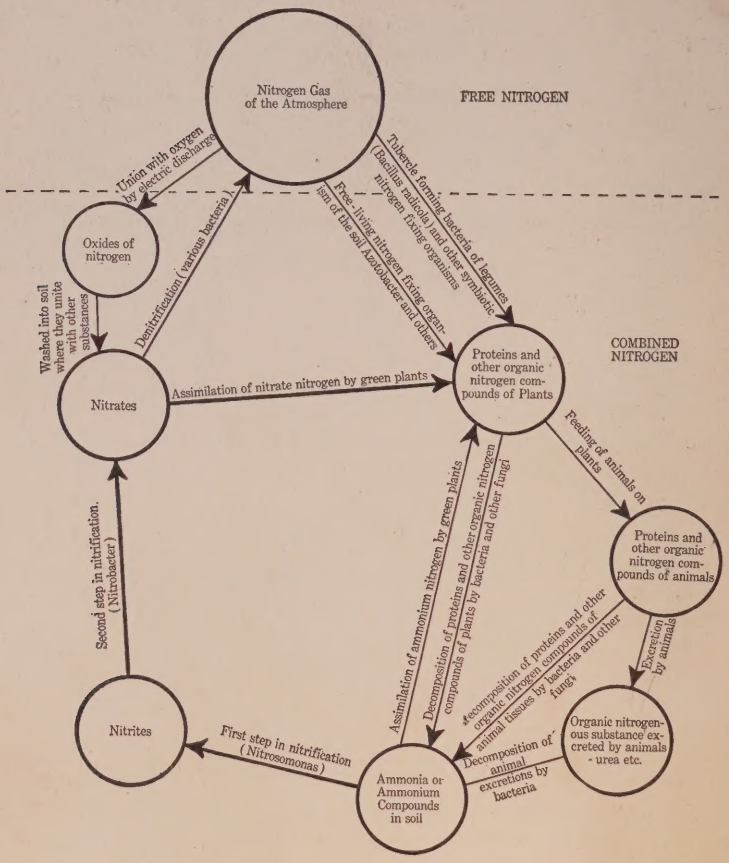

FIG. 128. — Diagram to show nitrogen cycle. Compare Fig. 127. (From Holman and Robbins.)

leaves or even the dead bodies of small animals. The grubs or larvae of many different types of insects, as well as some adult forms, have the same general habits. On the surface, other types of insects and related forms are found, of both herbivorous

and carnivorous habits. If a body of water is near, some amphibia, such as the wood frog,[3] and some of the salamanders and newts, all insect eaters, will be found. A few snakes occur, feeding on amphibia, the larger insects, smaller mammals and eggs of surface nesting birds. The smaller mammals such as the woodmouse, an insect and seed eater, spend most of their life on the surface or in their shallow burrows. Some of the herbivorous mammals ranging in size from rabbits to deer are classed as influents. But the life of the forest depends on the trees. And as we ascend the trunk different strata are sharply differentiated. Insects of all kinds swarm up and down in the crevices of the bark, many actually boring into the deeper layers; others are leaf eaters. Tree-frogs and toads spend the whole of their existence except at the breeding season and during hibernation upon the trees, feeding upon the insects that occupy the same strata. Squirrels nest in the trees and store the nuts collected in the fall. Larger carnivorous mammals, skunk, martens, and bobcats, visit the trees in search of their prey, mainly squirrels and nesting birds. The black bear, largest of the forest subinfluents, has an omnivorous diet ranging from insects and their grubs to the tips of succulent plants, and not omitting small mammals, birds' eggs, or the stored honey of the bee. Birds of all kinds, seed eaters, insect eaters, and predacious forms such as the owls and hawks abound. Considering the intricate relationships between these varied forms, ecology has well been termed the study of the web of life.

Development of the Community. — The community grows by immigration. Plants move by the dispersal of their seeds; animals have the power of locomotion. Inasmuch as animals must draw their food directly or indirectly from plants, the first step in the growth of a new community lies in the arrival of seeds by dispersion. The germination of the seeds is followed by the rapid extinction of all those which require the shade of other plants for further growth. But once a few species of hardy plants have won a foothold, these serve in the following season to protect a few others while they establish themselves. In this way the flora of the region commences its development, continuing until finally shrubs are established and afford shelter for the seedlings and saplings of the forest. This slowly evolves through long periods of years until the largest, most highly organized, and best-adapted trees come into a state of equilibrium

[3] *Rana sylvatica.*

with the climatic conditions of the environment. Such a community is called a **climax** community.

Meantime animals have been straying in and out of the area. We distinguish at least three levels of animal life, subterranean, terrestrial, and arboreal. Darwin has given us an excellent

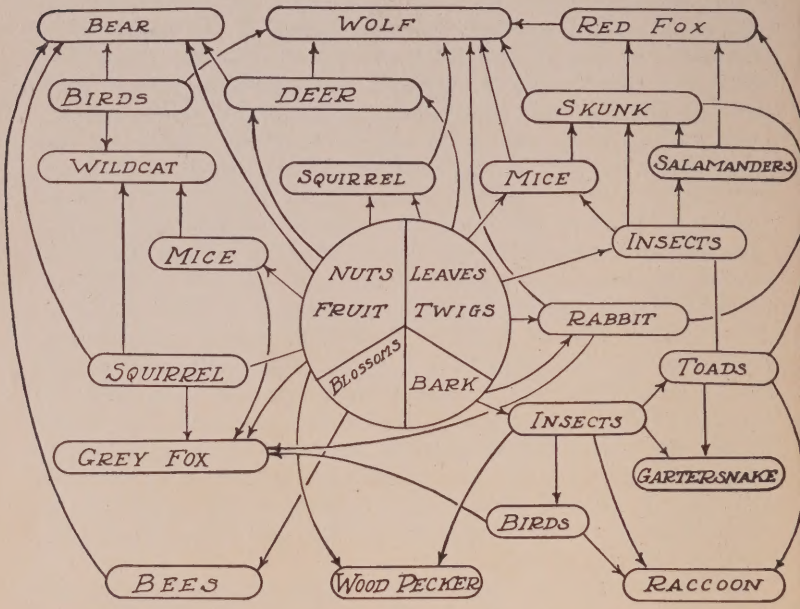

FIG. 129. — Diagram to show equilibrium in food relations of a forest community. The arrows point from the organisms used as food to those which prey upon them. The central circle represents the tree which is the dominant of the community. (After Shelford.)

picture of the activities of the earthworms in his "Vegetable Mould and Earthworms," showing how they constantly bring the lower layers of the soil to the surface and bury objects above the surface. He estimated that there were over 25,000 worms to the acre in the area he studied and that they raised a layer of earth $1\frac{1}{2}$ inches in depth, equivalent to 150 tons to the acre in the 10-year period covered by his studies. The subterranean forms come in relatively early in the life of the community. Terrestrial forms are found only when the flora affords an adequate food supply. Small insects of many types are the first arrivals.

Arboreal forms — we use the term to include all animals living above the surface of the ground — also arrive when food and particularly shelter are available.

As soon as a year-round source of food is established by the plant dominants, the animal predominants locate in the com-

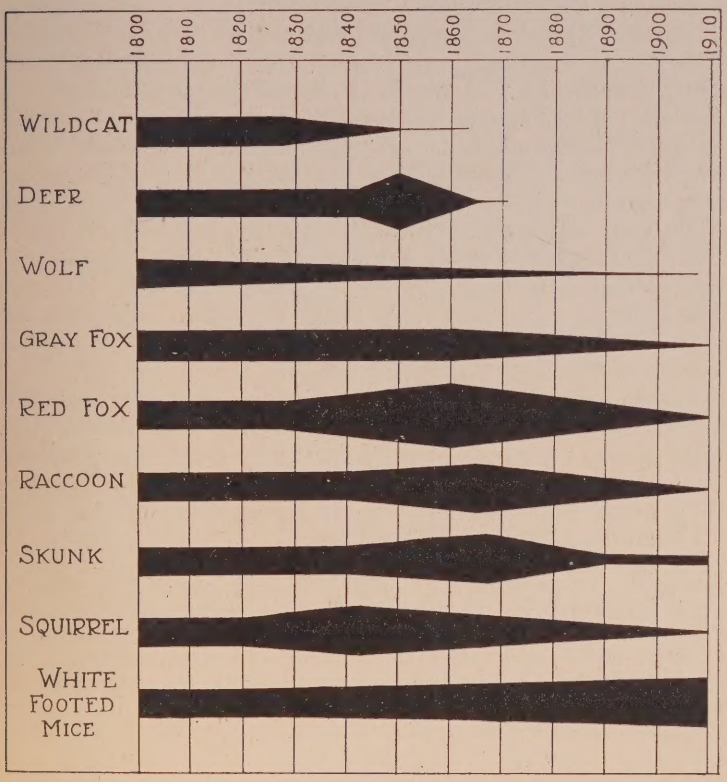

FIG. 130. — Diagram to show the changing mammalian population of Champaign County, Illinois, during the 19th Century. Note the sudden increase in the number of deer (1850) following decreases in the number of wildcats and wolves. (After Shelford.)

munity. From now on the growth of the community is governed by the new species of plants and animals which enter the community first as influents and subinfluents, and later, if they are able to acclimate themselves to the conditions of the community,

as dominants and predominants. So the community slowly marches to its climax.

Here it will maintain itself so long as the climatic conditions are unaltered in a state of perfect equilibrium between its external and internal factors. But over long periods of time major climatic changes have occurred and are to be expected. With these have come changes in plant and animal life almost catastrophic in their magnitude. The accompanying table shows the effect of an increasing human population upon the mammals of Champaign County, Illinois.

Aquatic Communities. — It is convenient to distinguish between fresh-water and marine communities, and we shall use the term **aquatic** to refer to the former, although in the larger sense it includes all water communities. Here temperature, light, water pressure, and currents make up what is called the subaquatic climate. This is of course variable, grading from surface conditions to the deepest depth of water. The chemical constitution of the water, particularly its hydrogen-ion concentration, is of great importance.

A Lake Community. — In his monograph on " The Lake as a Microcosm," the late Professor Stephen A. Forbes has set forth some general concepts of the life in the fluviatile (river-derived) lakes of Illinois which illustrate the biotic relationships between the different adaptation types so clearly that they are quoted in the following paragraphs.

> The amount and variety of animal life contained in them as well as in the streams related to them is extremely variable, depending chiefly on the frequency, extent, and duration of the spring and summer overflows. This is, in fact, the characteristic and peculiar feature of life in these waters. There is perhaps no better illustration of the methods by which the flexible system of organic life adapts itself, without injury, to widely and rapidly fluctuating conditions. Whenever the waters of the river remain for a long time beyond their banks, the breeding grounds of fishes and other animals are immensely extended, and their food supplies increased to a corresponding degree. The slow or stagnant backwaters of such an overflow afford the best situations possible for the development of myriads of Entomostraca [microscopic crustacea], which furnish, in turn, abundant food for young fishes of all descriptions. There thus results an outpouring of life — an extraordinary multiplication of nearly every species, most prompt and rapid, generally speaking, in such as have the highest reproductive rate, that is to say in those which produce the largest average number of eggs and young for each adult.

The first to feel this tremendous impulse are the protophytes and Protozoa, upon which most of the Entomostraca and certain minute insect larvae depend for food. This sudden development of their food resources causes, of course, a corresponding increase in the numbers of the latter classes, and, through them, of all sorts of fishes. The first fishes to feel the force of this tidal wave of life are the rapidly breeding, non-predacious kinds; and the last, the game fishes, which derive from the others their principal food supplies. Evidently each of these classes must act as a check upon the

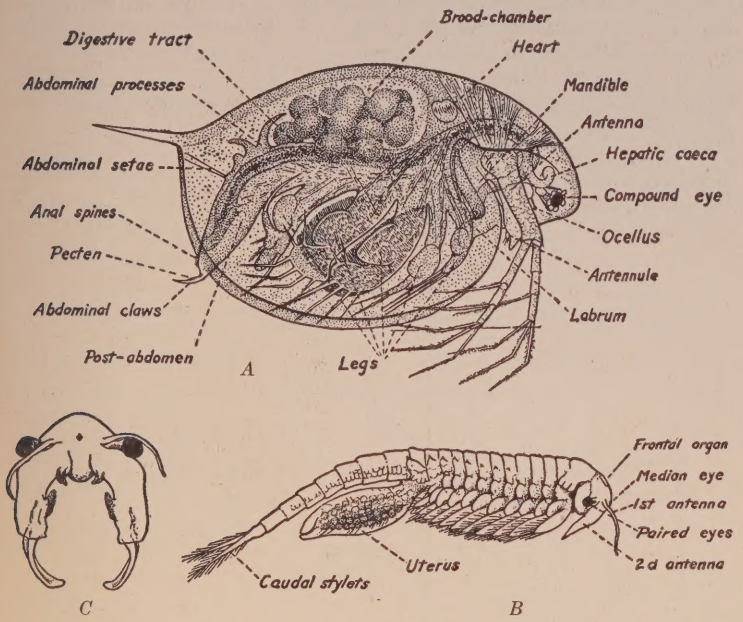

FIG. 131. — Entomostraca. Above, *Daphnia pulex*, the water flea; below, *Branchinecta packardi*, the fairy shrimp, anterior view of male (left), and lateral view of female (right). (After Dodds, from Curtis and Guthrie.)

one preceding it. The development of animalcules is arrested and soon sent back below its highest point by the consequent development of Entomostraca; the latter, again, are met, checked, and reduced in number by the innumerable shoals of fishes with which the water speedily swarms. In this way a general adjustment of numbers to the new conditions would finally be reached spontaneously; but long before any such settled balance can be established, often of course before the full effect of this upward influence has been exhibited, a new cause of disturbance intervenes in the *disappearance of the overflow*. As the waters retire, the lakes are again

defined; the teeming life which they contain is restricted within daily narrower bounds, and a fearful slaughter follows; the lower and more defenceless animals are penned up more and more closely with their predacious enemies, and these thrive for a time to an extraordinary degree. To trace the further consequences of this oscillation would take me too far. Enough has been said to illustrate the general idea that the life of waters subject to periodic expansions of considerable duration, is peculiarly unstable and fluctuating; that each species swings, pendulum-like but irregularly, between a highest point and a lowest point, and that this fluctuation affects the different classes successively, in the order of their dependence upon each other for food.

The Black Bass as a Predominant. — Professor Forbes continues:

As one example of the varied and far-reaching relations into which the animals of a lake are brought in the general struggle for life, I take the common black bass. In the dietary of this fish I find, at different ages of

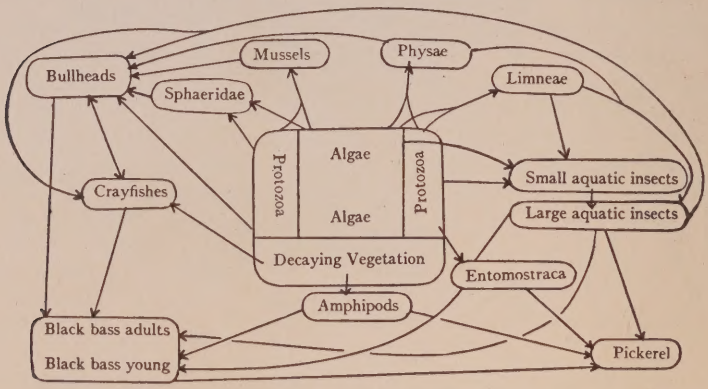

FIG. 132. — Diagram to show equilibrium in food relations of a lake or pond community. The arrows run from the organisms used as food to those which prey upon them. The Sphaeridae, mussels, Physae and Limneae are molluscs; the Amphipods are crustaceans. (From Shelford, "Animal Communities in Temperate America.")

the individual, fishes of great variety, representing all the important orders of that class; insects in considerable number, especially the various water-bugs and larvae of may-flies; fresh-water shrimps; and a great multitude of Entomostraca of many species and genera. The fish is therefore directly dependent upon all these classes for its existence. Next, looking to the food of the species which the bass has eaten, and upon which it is therefore

indirectly dependent, I find that one kind of the fishes taken feeds upon mud, algae, and Entomostraca, and another upon nearly every animal substance in the water, including molluscs and decomposing organic matter. The insects taken by the bass, themselves take other insects and small Crustacea. The crawfishes are nearly omnivorous, and of the other crustaceans some eat Entomostraca and some algae and Protozoa. At only the second step, therefore, we find our bass brought into dependence upon nearly every class of animals in the water.

And now, if we search for its competitors we shall find these also extremely numerous. In the first place, I have found that all our young fishes except the Catostomidae [suckers] feed at first almost wholly on Entomostraca, so that the little bass finds himself at the very beginning of his life engaged in a scramble for food with all the other little fishes in the lake. In fact, not only young fishes but a multitude of other animals as well, especially insects and the larger Crustacea, feed upon these Entomostraca, so that the competitors of the bass are not confined to members of its own class. Even molluscs, while they do not directly compete with it do so indirectly, for they appropriate myriads of the microscopic forms upon which the Entomostraca largely depend for food. But the enemies of the bass do not all attack it by appropriating its food supplies, for many devour the little fish itself. A great variety of predacious fishes, turtles, water-snakes, wading and diving birds, and even bugs of gigantic proportions destroy it on the slightest opportunity. It is in fact hardly too much to say that fishes which reach maturity are relatively as rare as centenarians among human kinds.

Marginal Communities. — At the shore line the life of the aquatic community is intimately connected with the life of neighboring terrestrial communities, for the boundary shifts with minor seasonal fluctuations and the more gradual but relatively permanent march of geological changes. Amphibious forms such as the frogs, snakes, and turtles, water birds, and mammals, i.e., the herbivorous muskrat and carnivorous otter, are subinfluents in this type of community.

Similarly the seashore marks a transition belt between terrestrial communities and the teeming life of the sea. The tides rising and falling twice a day create extensive areas in which many different types of communities are found, varying according to the climate, currents, and character of the coast. Thus there are sand flats, mud flats, rock pools, etc., each characterized by plant and animal adaptation types, although the particular species identified differ in different geographical regions.

Marine Communities. — Over three-fifths of the earth's surface is covered by the oceans, and a corresponding variety of com-

munities exists. The physical factors of the subaquatic climate are light, heat, pressure, chemical composition, and currents.

Light. — Light is of greatest importance at the surface. Its penetration varies according to the chemical composition of the water, particularly with reference to the substances in solution or suspension at the mouths of the great river systems. In the mid-ocean, where the chemical composition, salinity, etc., is most uniform, the red rays penetrate not more than 3000 feet and no sunlight penetrates more than 5000 feet. As four-fifths of the

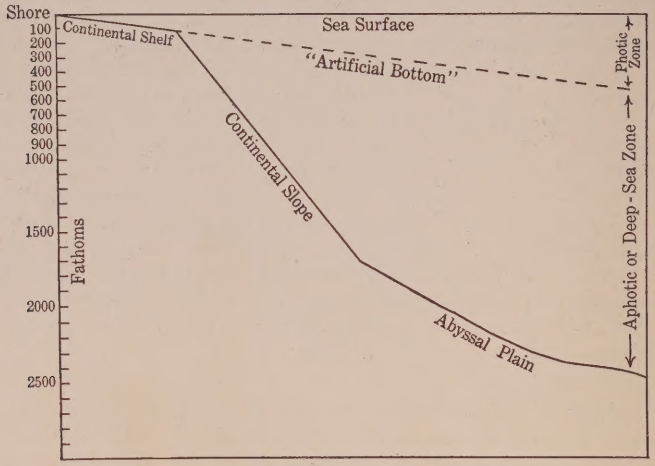

Fig. 133. — Diagram to the biotic areas of the ocean. (After Sir John Murray.)

ocean is more than a mile in depth, no light can exist on the ocean floor except the feeble phosphorescence of decaying organic matter.

Temperature. — The temperature too is more variable at the surface, and greatest of course in the equatorial belt. At both poles the great ice caps are continually cooling the waters as the ice melts. The resulting temperature gradients result in great movements of the waters, directed by the land masses at the margins and beneath the surface of the oceans, pulled by the rotation of the earth and to some extent influenced by the prevailing winds. One of these movements, known as the Gulf Stream, exerts a notable influence upon the biota of the North Atlantic. As the heat of the ocean like the light is primarily

affected by the radiant energy of the sun, there is another temperature gradient from the surface to the floor which is at a temperature close to the freezing-point.

Water Pressure. — The pressure of the water is a greater factor than is the atmospheric pressure in land communities. As has been said above, four-fifths of the ocean is more than a mile in depth; two-thirds is more than two miles; and the greatest depth ever sounded is over five miles. The air pressure at the surface is approximately 15 pounds per square inch. This is known as one **atmosphere.** This pressure is doubled at 35 feet beneath the surface (two atmospheres) and increases at the same rate to greater depths. The pressure at two miles then is roughly 300 atmospheres or 4500 pounds per square inch. As animals have been dredged at depths of from two to three miles, this pressure constitutes one of the prime physical factors affecting the community.

Salinity. — The chemical constitution of sea-water is marked by its salinity.

Marine Types. — Based on the physical factors listed above as well as the **hydrographic** features (topography of the sea bottom), three major community types may be distinguished: those of the shore (**littoral**), the surface (**pelagic**), and the floor (**benthic**).

Fig. 134. — *Postelsia*, a colonial green alga, which simulates a tree. (From Holman and Robbins.)

Littoral. — Littoral communities exist at depths from just below the low-water mark of the tides to 150 feet. They are characterized by their dominant plants, the seaweeds or marine algae, which vary from unicellular types to large and differentiated forms which simulate trees, like the remarkable *Postelsia* (Fig. 134). The green algae thrive best in the shallower waters; the browns in the deeper belt. This luxuriant vegetation supplies the initial food supply of a wealth of animal forms representing nearly

every division of the animal kingdom, the variety of which can be appreciated only by those who have had the opportunity of seeing it for themselves. It is for this reason that the biologists of the world gather periodically at one or another of the many marine biological laboratories which occupy strategic points on the boundary between land and sea.

Pelagic. — From river mouth and seashore alike great quantities of organic material are being swept out to the open sea, largely as nitrogenous waste, to form the primary food source for the construction of proteins by the plants of the ocean or pelagic communities.

Plankton. — The microscopic plants and animals suspended in water make up what is known as the **plankton,** in fresh water and ocean alike. But the plankton of the ocean is more varied in the forms of life which it includes. The unicellular plants (**phytoplankton**) are found throughout the photic zone, often found " in the form of vast floating meadows," to use Sir John Murray's expressive phrase. These are composed principally of brown algae, in which the chlorophyll is masked by the other pigments of the plastids. Another group found in abundance in the plankton are the dinoflagellates, claimed by zoölogist and botanist alike. The phytoplankton of the photic zone build up from inorganic compounds their own protoplasm, the organic compounds of which serve as food for the other denizens of the deep. Herbivorous animals feed on the phytoplankton, and these in turn become the prey of carnivores.

Animal Plankton. — The **zoöplankton** includes equally large numbers of protozoa, mainly radiolaria (with siliceous skeletons), and foraminifera (Fig. 170, *A*), whose tests of calcium carbonate go into the making of chalk. The jellyfish (Fig. 172) represent the coelenterates. The most abundant of all pelagic animals, however, are the smaller crustacea (Entomostraca). Some molluscs and tunicates (Fig. 188) are found in quantities. The remainder of the plankton is made up of larvae of coelenterates, worms, crustacea, molluscs, tunicates, and fish. All these feed on the phytoplankton and smaller forms of the zoöplankton.

Nekton. — But the real predators are those which have the ability to swim against the surface currents in which the plankton proper are passively carried along. These forms, known collectively as the **nekton,** include cuttlefish, such as the octopus, many kinds of true fish, reptiles, such as the sea-turtles, some marine birds and even mammals, e.g., the whale.

Benthos. — The benthos comprises the plants and animals of the deep seas or abyssal zone. It is characterized by the entire absence of photosynthetic plants. Their dead remains, however, fall through the abyssal depths like manna, furnishing food to animals of all sorts on the way down and on the bottom itself. These remains undergo decomposition brought about by the activity of bacteria. Putrefactive, nitrifying, and denitrifying bacteria are found in the ocean as well as on the land. The bottom level of the photic zone is known as the **artificial bottom,** and may be regarded as a continuation of the mudline of the continental slopes. Here the falling particles are stayed through changes in the physical conditions, viscosity, etc., and afford a rich feeding ground for the nekton, which come from both pelagic and abyssal zones.

Deep-Sea Animals. — Many bizarre and curious animals have been dredged and hauled from the depths of the sea. Little is known, however, of these deep-sea communities, first because of the difficulties of collection, and second because, although these animals withstand the tremendous pressures of the abyss, they are exploded by the compressed gases of their own bodies when the pressure is rapidly diminished. One can imagine the value of a census taken on land by drawing a net behind an airplane traveling a mile in the clouds. But it is on just such evidence that we must draw our conclusions as to the life of the benthos.

Whether in the deep sea, lake, or forest, organisms exist only as members of a community. Their existence depends upon their adaptation to the complex interrelationships existing among the plants and animals of the community, the local conditions in which the community is found, and the larger climatic factors governing its development. The species represented in the community hold their place only as the individual organisms of that species are able to maintain and reproduce themselves in the ecological web of life.

CHAPTER IX

THE EVOLUTION OF SPECIES

In the two chapters immediately preceding we have been concerned with problems particularly concerning the species. In the study of heredity, the conception of the gene serves to explain how plants and animals always reproduce after their kind, even though the individuals of that kind may show distinguishable differences. The genes are the internal factors whereby the members of a species are bound together in ties of common kinship. In the study of ecology the conception of the community has indicated how the members of each species within the community are affected not only by the climatic and edaphic factors but by their relationships with every other species represented. The species then has its external relationships as well as its internal relationships.

Conservatively estimated, there are well over a million species of plants and animals. Naturally enough these are scattered all over the world, and as explorers open up new territories and naturalists collect specimens of the new fauna and flora to be found in each, new species are constantly being added to the list. What can we say concerning the origin of these varied forms of life? Have they always been the same? There are two hypotheses in answer. The first is that every species was created separately and will continue as such indefinitely, a conception essentially static. The second hypothesis is that species come into being from older species, that they develop and grow, compete with other species, wax old and die, a conception that is truly dynamic. The first theory, that of **special creation** and the **fixity of species,** was perhaps tenable in the days when relatively few species were recognized. Today it is completely replaced in scientific literature by the second theory, that of **evolution.**

THE THEORY OF EVOLUTION

These opposing concepts, static and dynamic, may be traced back through the writings of ancient philosophers. Aristotle had a theory that changes were caused by an internal perfecting tendency.

And a vague idea of evolution pervaded the writings of that great Roman philosopher-poet Lucretius. But it was not until the nineteenth century that any theories concerning the evolutionary process attracted widespread attention. In 1801 Lamarck published his theory that all existing species, including man, were descended from earlier species, a conclusion to which he was led by the difficulties he encountered in trying to classify the collections of the Jardin des Plantes at Paris, of which he was the Director. Later in 1809 and in 1815 he elaborated his theory, which we shall merely indicate at this time and return to later. He held that each organism strove to adjust itself to its surroundings, that in so doing new structures were developed, strengthened by use, weakened or eliminated by disuse, and that the changes so induced were transmitted to the offspring.

Natural Selection. — In 1859 Charles Darwin published "The Origin of Species by Means of Natural Selection, or The Preservation of Favored Races in the Struggle for Life." During the past seventy years the discussion of this theory has held the center of the biological stage. From the moment of its publication to the present day, the theory of natural selection has had its ardent supporters and its no less bitter opponents. But whether or not natural selection is proved to be the causal agent in evolution, the great mass of facts accumulated by the partisans on either side has resulted in a logical demonstration that species are the result of evolution.

Darwinism. — It is perhaps unfortunate that Darwinism has come to have three separate connotations. To the professional scientist the word means the theory of natural selection; to the average reader it is synonymous with the theory of evolution; and there are still some to whom the word conveys only a crude idea that men are descended from monkeys. There are three separate questions involved: first, whether evolution by means of natural selection is a satisfactory hypothesis; second, whether or not the evidence for the existence of evolution is satisfactory; and third, what has been the course or history of evolution.

The concluding paragraph of "The Origin" sums up Darwin's argument:

> It is interesting to contemplate a tangled bank, clothed with many plants of different kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have

all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character, and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

Ratio of Increase. — Darwin's figures to show that the ratio of increase must be balanced by natural checks have often been cited. He quotes Linnaeus to show that if a single plant produced but two seeds a year, and each of these germinated and gave rise to a plant producing two seeds, at the end of twenty years there would be well over a million plants ($2^{20} = 1{,}048{,}576$). And there are plants which produce 75 million seeds in one year. One fern in the tropics may form 200 billion spores in a season. The slow-breeding elephant does not mature till thirty and the female bears young about once in ten years. Assuming that the elephant lives till the age of ninety, a single pair would give rise to nearly 19 million descendents in 750 years. The oyster may produce 60 million eggs in a season. Assuming the average number to be 16 million, and that all develop and give rise to males and females in equal numbers, which continue to reproduce at the same rate, in five years the bulk of the shells would be more than eight times that of the earth. Woodruff's race of *Paramecium* produced over 12,000 generations in twenty years. At the end of five years he calculated that the bulk of protoplasm produced ($2^{3000} \times$ the bulk of a single *Paramecium*) if all the protozoa could have been kept alive would have been 10^{1000} times the volume of the earth. But of all organisms the bacteria have the most prolific birth-rate. Reproducing asexually every half hour, in a single day there would be 2^{48} descendants from a single bacterium, with a combined weight of half a million pounds.

Struggle for Existence. — This potential rate of increase is kept down, however, by natural checks and balances, as we have seen in the preceding chapter. Darwin noted the seedlings of common weeds which came up on a plot of land three feet long and two

feet wide which had been dug and cleared, and discovered that "out of 357 no less than 295 were destroyed, chiefly by slugs and insects." Comparatively few of the enormous numbers of seeds produced by plants or the eggs laid by animals ever come through to maturity. Yet the species persist and hold their places in the life of the community. Darwin pointed out that if a tree lived for a thousand years, the number of the species could be maintained if but a single seed were produced during that period, provided that seed grew to maturity unmolested.

From these two well-established facts, the fertility of all forms of life, and the struggle for existence that ensues, Darwin drew the conclusion that there was a differential survival rate.

He had long made a study of the practices of plant and animal breeders and noticed that from their stocks they selected certain forms only which they allowed to breed. This system permitted them to preserve characteristics which they desired and to eliminate characteristics which they thought undesirable. To the struggle for existence in nature Darwin ascribed a similar selective action. But what was the basis of selection in nature?

Variability. — Darwin first called attention to the variability of characters within the species, and devoted a great deal of attention to demonstrating the existence of minor differences. As we have seen in our study of Genetics, biologists today ascribe very many of these to mutations, i.e., changes in the constitution of the gene, or to aberrations in the number of chromosomes or in part of a single chromosome, which are inherited according to the laws of genetics. These allelomorphic characters are sometimes called discontinuous, because of the contrasts that exist between them, and their segregation in inheritance. Many other minor differences exist, chiefly in the size and number of parts, which can be arranged in an intergrading series. These are called continuous variations.

Biometrics. — Some of these may be due to very slight modifications in a single gene or in a complex of genes. But owing to the difficulty of handling these data by the ordinary methods of genetic analysis, they are studied by other statistical methods, which have developed into the science of **Biometrics.**

Frequency Curves. — The accompanying figure (Fig. 135) of a pailful of scallop shells will serve to illustrate the method as applied to a single character, i.e., the number of ribs per shell. There are five classes of shells ranging from 15 to 19 rays each.

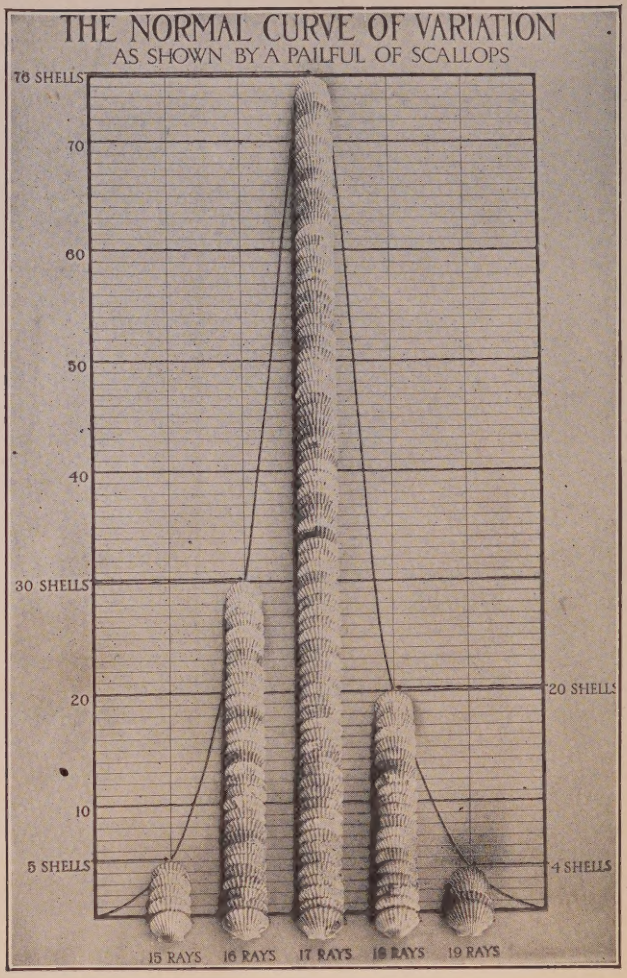

FIG. 135. — Variation in the number of rays found in scallop shells. (Photograph by American Museum of Natural History, from Curtis and Guthrie.)

The number of individuals in each class (frequency distribution) is 5, 30, 76, 20, and 4, respectively. By arranging these in order, with the ordinates representing the frequencies, and the abscissae representing the series of classes, a curve may be drawn which

corresponds to a probability curve. This curve has a single mode (or high point representing the greatest frequency) which is in the mean or average class represented. In a population with continuous variations affected equally by a large number of factors, the frequency curve will be very close to the mathematical probability curve. Aberrations indicate the existence of fewer factors with unequal influence. Among such aberrations are curves with one or more modes, differences between the mode and the mean (skewness), etc. Bimodal curves usually indicate the existence of a mixed population of two main types; skewness may be taken to mean the preponderance of one set of factors over others, etc.

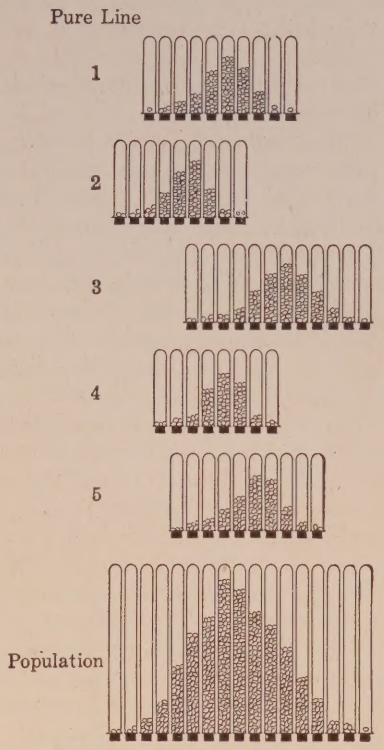

FIG. 136. — Diagram to show variations in weight of five pure lines of beans, and in the population composed of all five. (After Johannsen, from Walter, "Genetics," The Macmillan Co.)

Pure Lines. — An example of the usefulness of the statistical method is Johannsen's work on beans. He selected the heaviest seeds to germinate for a new generation. The plants obtained were self-pollinized, and the seed of each weighed and counted. The frequency curves so obtained fell into a number of classes which he called **pure lines.** The seed from any given pure line produced always the same frequency curve, no matter whether a light or heavy seed was selected for the starting point. But if seeds from the different lines were lumped in one mixed population a seed chosen from the lightest class might give a frequency curve quite different from one chosen from the heaviest class. In other words, his selection brought out only the different hereditary pure lines of which the population was

composed. The differences within the pure line are non-inheritable and due solely to the effects of the environment.

We must distinguish then between hereditary variations (due to differences in the genes) and non-inheritable variations (due to differences in the environment). The first type are of importance in evolution, as they are transmissible. The second type are of importance only as they affect the life of the individual and increase or decrease the probability of reproduction and the transmission of the heritable characters of the pure line to which it belongs.

Variation and Survival Value. — Granted then, indeed it has been amply demonstrated, that there are two types of variation with regard to heritability, are these variations sufficiently important to affect the success of the organism in the struggle for existence? It has been urged that the variations are seldom great enough to have a survival value, and that selection takes place early in the life history before the individual characters of the adult have appeared. The answer to both of these objections seems to lie in the behavior of the gene. As pointed out on page 177, the gene affects many of the structures and activities of the cell, but only a few of the changes are visible. Thus the gene which produces white eye-color in *Drosophila* also lessens the fertility, slows the rate of development, and decreases the viability of the fly. The white eye-color, therefore, although not in itself a survival factor, is the visible indicator of a change which lessens the chances of survival in the flies so distinguished. Many genes like this may produce developmental disharmonies, which affect the chances of the individual's arriving to maturity in addition to the visible changes produced in the adult. We know practically nothing about the physiology of the gene, that is to say, the way in which the gene produces its effects. But in that infinitely complex set of chemical changes characteristic of protoplasm, a single internal change such as that involved in the mutation of a gene will inaugurate a disturbance which may have an adaptive significance.

Inheritance of Acquired Characters. — It is of course true, as Darwin pointed out, that very small differences may make a profound difference in the chances of survival in the struggle for existence. But many of these small differences are due to environmental influences rather than to genetic changes and therefore are not inherited. It has been pointed out, however (page 179), that the theoretical possibility exists of similar changes oc-

curring simultaneously in the soma and the germ cells because of a mutation in a gene during one of the early divisions of the egg.

The idea expressed by Darwin, and by Lamarck before him, that use and disuse play a part in the development of variations, is generally admitted, but that such variations are inherited is as generally denied. This is of particular importance in connection with the alleged inheritance of mental traits, for if conditioned reflexes (see page 115) are developed by the continued use of particular synapses, they would not appear to be heritable.

Divergence. — Let us now consider the effect of natural selection upon species in which mutations are taking place. Obviously the more violent mutations will as a rule fail to survive, because they will seldom be of advantage to the animal or plant concerned, even if they are not lethal. Thus we find few albinos (unpigmented) animals in nature. Although the white mouse, a true albino, is extensively bred in captivity, it cannot compete with the normal type under natural conditions. Natural selection tends to hold the species true to type and allow only those mutations to survive which are of adaptive significance, or at least not disadvantageous. But if a mutant race does survive and breed, its establishment will result in what Darwin called divergence of character between the two stocks. Thereafter new mutations in both stocks will bring about new genetic complexes, and an accumulation of genetic differences. In this way stocks differing in various characteristics would arise to compete with each other in the struggle for existence, and each would be sufficiently distinctive to merit the rank of species.

Migration and Isolation. — There are several possibilities as to the future. The two species may occupy the same area if the differences between them are sufficiently great that they occupy different positions in the community — say, that the differences involved a slight divergence in diet. The second possibility is that one species survives while the second becomes extinct. A third is that each species migrates or is distributed in all directions from the community in which it originated and so finds its way into new environments to some of which the new species is better adapted, while in other localities the older species is more successful. In other words, successful variations may become successful varieties, and these may give rise to successful species, while competitive variations, varieties, and species are driven out to seek new habitats or are rendered totally extinct. Successful species multiply and spread out in all directions so that

they come in competition with the local (indigenous) species found in other communities. In this way the community is exposed to new biotic influences and the species represented in the community are subjected to new rivals in the struggle for existence.

Barriers to Migration. — Strictly terrestrial organisms cannot pass large bodies of water, and the migration of fresh-water organisms is blocked by land masses and oceans alike. The migration of marine forms is delayed but not necessarily prevented by the continents. The migrations of birds and insects are limited chiefly by their powers of flight. These geographical barriers are supplemented by other physical factors, particularly by those of climate. Thus cold climates act as barriers to organisms which are adapted to the tropics, etc.

Isolation and Species Building. — One of the older criteria employed to test the validity of species was based on the theory that members of separate species could not be bred together or that the offspring would be sterile. This theory has long been disproved in the original form, for species as diverse as cattle and buffalo have been successfully hybridized. But the inability of varieties to breed together because they are isolated from each other is certainly one of the important factors in the establishment of separate species which might be merged in a general population if interbreeding continued.

In addition to geographical isolation, physiological isolation must be taken into account. By this is meant such inability to interbreed as is caused by differences in the reproductive period, especially noticeable in the plant kingdom. When different varieties of the same plant species flower at different times, they cannot breed together even if growing side by side. Then, too, many species are unable to produce viable or fertile hybrids owing to the fact that the chromosome number is different in the two species concerned (the mule) or possibly to the antagonistic action between the genes which each contributes. The longer such isolation continues the wider the separation between the two species will become.

THE EVIDENCE FOR EVOLUTION

In the preceding pages we have seen how Darwin developed the theory of evolution through natural selection and how in the light of modern Biology this theory is to be interpreted in

terms of Genetics and Ecology. It now becomes our task to see whether the facts of Botany and Zoölogy accord with the theory. The lines of evidence which we shall examine are three in number: (1) from the geological succession, (2) from geographical distribution, and (3) from the comparison of the structure of plants and of animals (comparative morphology).

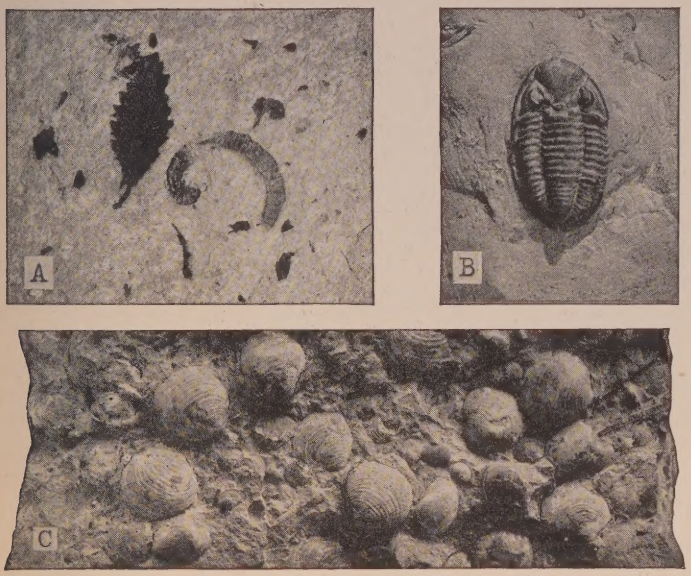

FIG. 137. — Fossils. A, impression of leaf (left) and insect larva (right); B, a trilobite (*Phillipsia griffithides*), one of the Arthropod classes now entirely extinct; C, shells, mostly *Astarte*, a marine clam. (Photographs by the American Museum of Natural History, from Curtis and Guthrie.)

Darwin opens the introduction of "The Origin of Species" with the following sentence, "When on board H.M.S. 'Beagle,' as naturalist, I was much struck with certain facts in the distribution of the organic beings inhabiting South America, and in the geological relations of the present to the past inhabitants of that continent." The study of geographic distribution and geological succession offer to this day the most convincing evidence that our present species are the result of evolution.

Geological Succession. — In and on the surface of the earth are found the remains of organisms long since dead, which are

called fossils. Sometimes these are hard parts such as the bones of vertebrates or the shells of molluscs, in which the calcium carbonate has been replaced by inorganic mineral salts. Sometimes molds are formed about softer parts and later filled with material which may be called natural casts. Both plant and animal material has been preserved often in such detail that botanists have been able to work out the anatomy of the embryo

Fig. 138. — Exposure of sedimentary rock. (From Pirsson and Schuchert.)

in fossil seeds and zoölogists to study the microscopic structure of bone. The study of fossil plants is known as **Palaeobotany,** and that of fossil animals is called **Palaeozoölogy.** The geologist who uses the fossils characteristic of the different layers of the earth as markers or index fossils, uses the term **Palaeontology** for the general study of fossils.

Strata. — The surface of the earth is made up of many layers, varying in depth, in the material of which they are constituted, the manner of their formation, and the fossils, if any, which they contain. These layers are called **strata.** A very large proportion of these were deposited one upon the other through the gradual settling down of suspended material in the ocean, lakes, and rivers. Sedimentary rocks (Fig. 138) of this kind are generally found in a series one upon another, with the oldest layers at the bottom, the youngest at the top. Although these layers and their relationships to one another differ in various regions

because of the movements of the earth's surface, the succession has been worked out to the point where it affords a reliable measuring rod for the more recent geological history. The thickness and character of the different layers afford a measure of the time required for the deposition of each, so that a chronological table can be constructed. In such geological charts the oldest period, like the layer to which it corresponds, is always placed at the bottom.

Chronology. — The chronological chart (Fig. 139) of geological period gives a synopsis of the course of evolution. The time scale is given in geological units. If the 60,000,000 units could be shown on a clock face representing the twelve hours from noon till midnight, the Cambrian period would begin at 6 P.M. In this period practically all the marine invertebrate phyla and representatives of all but the land plants are in existence. At twelve minutes of eight, the first land animals (amphibia) and plants (primitive ferns, club-mosses and horse-tails) are found. Reptiles and conifers are found at 9 : 45 P.M. Mammals and the flowering plants commence their existence at about 11 : 45. The 25,000 years of man's recorded history would consume only the last four seconds before midnight. But geologists estimate the value of a time unit up to twenty-five years, so that the length of time required for the formation of the rocks is approximately 1,500,000,000 years.

Many examples suggest themselves as illustrations of the palaeontological evidence. But perhaps the one most often employed is that of the horse in North America. This history has been so carefully studied and is so well documented that it has been frequently used in controversial discussions. Opponents of the evolution theory have often referred to the " stalking horse of evolution," but the facts are so convincing that it seems worth while to examine them in some detail.

Eocene Horses. — The first remains of fossil horses in North America appear suddenly in the Eocene period, approximately 55 million years ago. Since 1870, when the first Eocene horses were discovered in Wyoming, eight well-defined species of this genus *Eohippus* have been identified from the Wasatch beds in Wyoming and a similar locality in New Mexico. The smallest of these[1] stood less than ten inches high at the shoulder. Two other species of which practically complete skeletons have been assembled stood respectively eleven and twenty inches high. These

[1] *Eohippus index.*

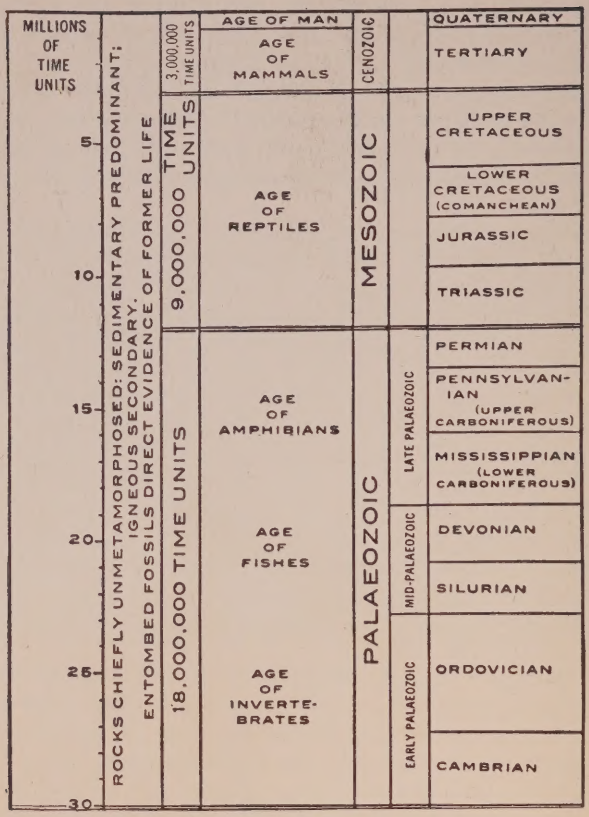

FIG. 139. — Geological time scale. First column shows the duration of each geological division in time-units. The second column indicates the general character of the rocks. The third lists the geological eras with their relative ages and characteristic animals. The last column gives the periods into which each era is divided. The Pre-Cambrian is at least as long as the divisions shown on the scale. The absence of fossils may be due in part to the metamorphic processes to which the rocks have been subjected. Compare Fig. 169 for characteristic plants of the eras. (After Osborn, from Curtis and Guthrie.)

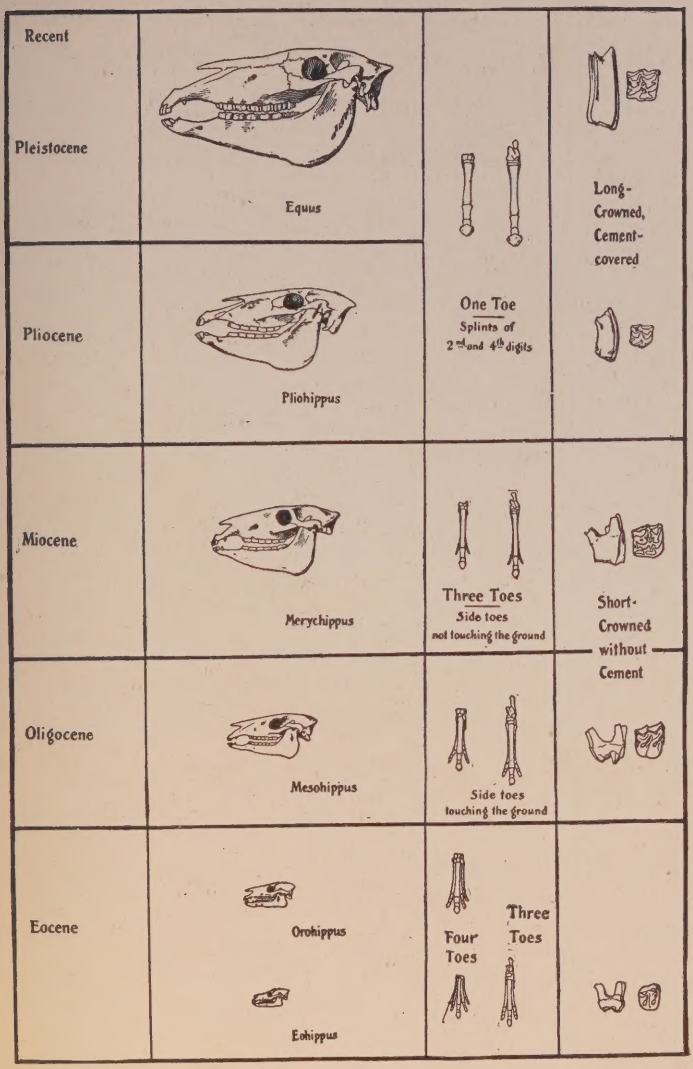

FIG. 140. — Diagram to show some of the principal steps in the evolution of the horse. First column, the divisions of the Tertiary, and Quaternary periods. Second column shows increase in size and particularly the length of the skull. Third column shows the increase in length of the leg and reduction in number of toes (fore leg on left). Fourth column shows increase in depth and complexity of molar teeth. The figures in second column are drawn to scale. (After Matthew, from Berry, "Textbook of Palaeontology," The McGraw-Hill Book Co.)

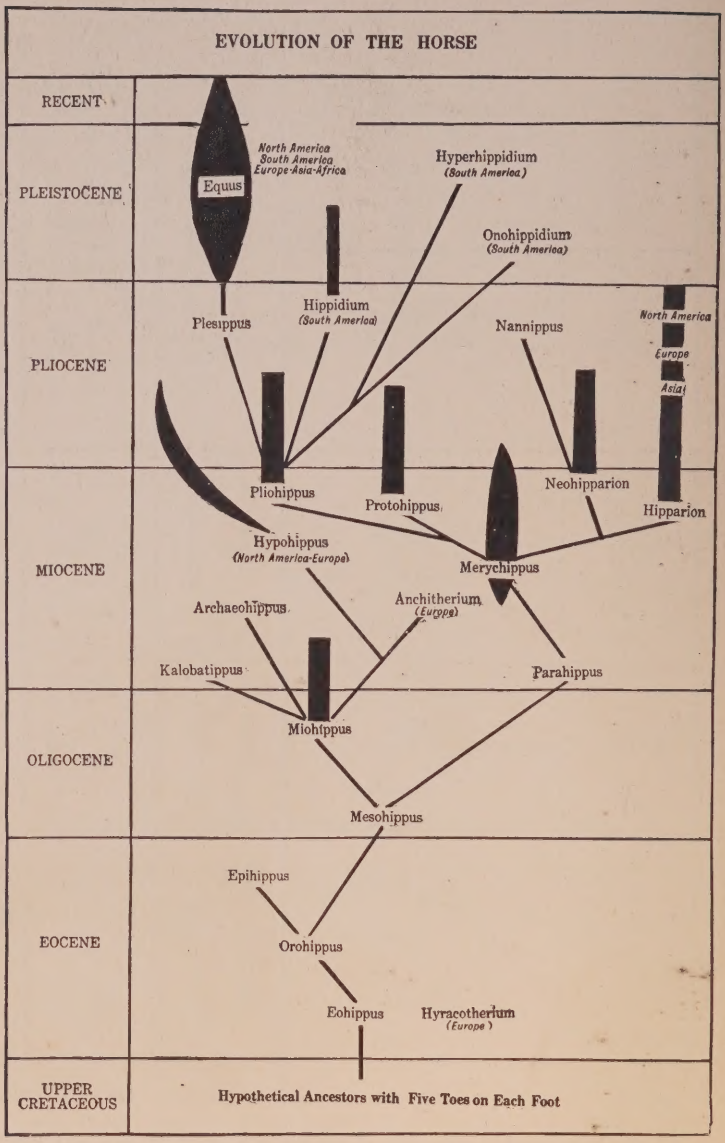

FIG. 141. — Diagram to show the genealogy of the principal genera of horses in North America. The thickness of the lines indicates roughly the predominance of the different genera. Note especially the genera mentioned in the text. (From Berry.)

little creatures would never have been recognized as horses were it not for the discovery of a series of intermediate forms linking them with the horse of today. The proportions of the whole body are unlike those of the modern horse. The fore-foot has four toes, the hind-foot has three, with traces of the first and fifth digits persisting as vestigial splint bones. The teeth are

FIG. 142. — *Eohippus*, painted by Charles R. Knight under the direction of Henry Fairfield Osborn. (Photograph by courtesy of the American Museum of Natural History.)

short-crowned, with four projections or cusps on the molar teeth (grinders) and no cement between them, much like the human molar.

The Eocene period was preceded by the Cretaceous, in which the grasses, the typical food of the horse family, first appear in geological history. But the horses of the Wasatch were still forest dwellers. Loomis, who has analyzed the fossils of these beds, pictures them as flood plains. The climate was warm, as is indicated by the presence of crocodiles and palm trees. The animals were of the woodland rather than of the prairie type. The restoration of these animals (Fig. 142) is based on careful studies of the skeleton over which the muscles are modeled.

This reconstruction of the muscles involves a painstaking comparative study of the muscles of the modern horse, and the adaptation of the data to the skeleton of *Eohippus*. Thereafter the features of the skin, hair, and color are largely conjectural. The background is filled in from studies of the palaeoflora of the period. A great deal of detailed knowledge drawn from different fields of specialization is required for such reconstructions, and their value depends upon the amount of detail available as well as the skill of the artist.

In the middle and late Eocene, two new genera, *Orohippus* and *Epihippus*, appear, in which the premolar teeth are developing the four cusps characteristic of the molars, and the middle digit (III) on both the fore- and hind-foot is enlarging. This enlargement of the middle digit is indicative of a gradual change from forest to plains life, as lengthening and strengthening the axis of the foot presages a lengthening of the leg and an increase of speed.

During the Eocene, fossil horses are also found in Europe, but there they showed a remarkable adaptability to different types of life and diet, with many species and at least eight genera, commencing with the earliest-known type *Hyracotherium*, comparable to the American *Eohippus*. Inasmuch as the horse appears so suddenly in both Europe and America with no immediate predecessor in the transitional Palaeocene period, it is believed that it migrated into both regions from a common starting point, possibly central Asia.

Oligocene Horses. — In North America the period following the Eocene is the Oligocene, best known from its exposures in the so-called Bad Lands of the West. These are made up of the dust from extended prairies and the flood plains of the sluggish rivers which made their way across the prairies. The palaeoflora indicates the existence of few trees and a warm climate. The characteristic genus of the period is *Mesohippus*, and its best-known representative *Mesohippus bairdi*. This species was about the size of a collie dog. The fore-foot had but three toes with a splint of the fifth digit (the fourth toe of *Eohippus*). The middle digit on each foot was still further enlarged and the legs longer in proportion to the body length than in *Eohippus*. The premolars are now like the molars, and on both the cusps are connected by longitudinal crests, thus strengthening the teeth for a diet of grasses. The skull is more elongate, the first premolar reduced, and the distance between the canine and the premolars increased. In the latter part of the Oligocene, species of *Miohip-*

pus, which continues into the next period, are found. This genus is distinguished by the increase in the length of the crown of the teeth, and the enlargement of the middle toe on both fore-

FIG. 143. — *Mesohippus*, a prairie horse. Painted by C. R. Knight under the direction of H. F. Osborn. (Photograph by courtesy of the American Museum of Natural History.)

and hind-foot. In Europe the horse became extinct during the Oligocene.

Miocene Horses. — The Miocene was the period in which the American horses displayed the greatest number of adaptive types. Commencing with the single genus *Miohippus* in the lower Miocene, at least ten genera are found before the end of the period. Two diverging lines of evolution are represented, one culminating in *Hypohippus*, the forest horse, whose short-crowned teeth and re-elongated side toes show him to have been a forest dweller, living on leaves and herbage. A collateral line made its way to Europe by way of Asia and died out in the lower Miocene. *Hypohippus* survived in North America until the following period, and the last species recorded is from the Pliocene forests of China. The other main line of evolution is represented by the mid-Miocene genus *Merychippus*, a group of some twenty-five species showing a progressive increase in size from earlier forms not much larger than a good-sized sheep to animals nearly the size of the modern horse. The molars increase in the length

of the crown and the development of transverse folds between the longitudinal crests, so forming lakes which are filled with cement. The middle toe is elongated so that the side toes do not touch the ground. Towards the end of the period three new genera arose from *Merychippus*, two of which at least show marked tendencies in the elongation of the leg, loss of the side toes, and increase in crown length, in other words, the development of a prairie type.

Fig. 144. — *Hypohippus*, a forest horse. Painted by C. R. Knight under the direction of H. F. Osborn. (Photograph by courtesy of the American Museum of Natural History.)

Pliocene Horses. — These reach their fuller development in the Pliocene. *Hipparion* represents one line which attained to the size of an ass but never lost the side toes completely. Indeed, in the Pliocene representative the side toes seem to be enlarging again as though in this period *Hipparion* was returning to the woodland. Early in the Pliocene this genus migrated into Asia, Europe, and Africa. It gave rise to a number of European species, some of which persisted almost to the end of the period. *Pliohippus*, on the other hand, lost the side toes completely and except for size (about that of a pony in the largest species) and

FIG. 145. — *Neohipparion,* a species very similar to the more widely distributed *Hipparion.* Painted by C. R. Knight under the direction of H. F. Osborn. (Photograph by courtesy of the American Museum of Natural History.)

the simpler pattern of the molar teeth resembled the modern horse. This genus gave rise towards the end of the Pliocene to the South American genus *Hippidium* and the true horse *Equus.*

Pleistocene Horses. — In the Pleistocene, or Ice Age, the continents of Europe, Asia, and North America were intermittently partially covered with ice-sheets, so that glacial periods alternate with interglacial periods. During this period, which occupied roughly a million years, over 45 species of *Equus* are distinguished in the different parts of the world, one of the more important North American species being *Equus scotti.* The common domestic horse is known as *Equus caballus.* Its immediate feral ancestor

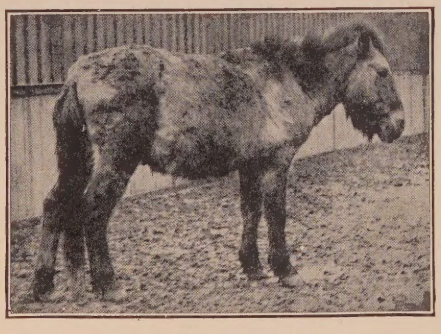

FIG. 146. — *Equus przevalskii,* the wild horse of Mongolia. (After Thompson, from Curtis and Guthrie.)

is unknown, the nearest wild horse being the Mongolian *Equus przevalskii* (Fig. 146).

Horses of Other Continents. — The fossil horses of Europe were first described by Baron Cuvier. An opponent of the evolution theory, he held that they were members of successive faunas which replaced those destroyed in former cataclysms. After Lyell and other geologists had overthrown the cataclysm theory, Huxley prepared a history of the evolution of the horse based solely on the European species. The discovery of the American species is the result of the expeditions sent out to accompany the surveying parties of the great transcontinental railroads, and later by the museums such as the American Museum of Natural History, and the museums of Yale, Princeton, Amherst and others. A vivid picture of the course of evolution is given to those who can study such collections for themselves.

In the preceding account of the evolution of the horse particular attention was paid to migrations of members of the horse family, from North America to Asia and thence to Europe in different geological periods, and particularly to the migration of *Hippidium* to that continent in the late Pliocene. The invaders found the continent in the possession of a local fauna which had developed free from competition with the fauna of the Northern continent because of the absence of a land bridge in the earlier periods of the Cenozoic age. In South America then there had arisen from the earlier Patagonian fauna adaptation types parallel to those of North America. The pampas was occupied by a "pseudo-horse," *Litopterna,* which was speedily displaced by *Hippidium* and the genera descended from it. These in turn were replaced by species of *Equus* which made their way in South America across the Isthmus of Panama in the Pleistocene.

Geographical Distribution. — These facts have a considerable importance in the study of modern geographical distribution. We must recognize that a prolific and varying species radiates in all directions from its point of origin. In those new regions from which it is not cut off by geographic barriers, it enters older communities. If it is adaptable to the new conditions it comes into equilibrium with the older species, but more often displaces the one with which it comes into closest competition for food. The existence of natural barriers to migration results in the limitation of competition to fewer competitors, and, within the species, to a larger degree of inbreeding and the consequent suppression of mutations. On this account we find many so-

called geographical varieties which may well be called species in the making. Darwin frequently commented on the fact that islands usually have indigenous faunas differing from each other as well as from the communities of the mainland. The factor of isolation by natural barriers then is to be considered one of the accessory factors in species-building.

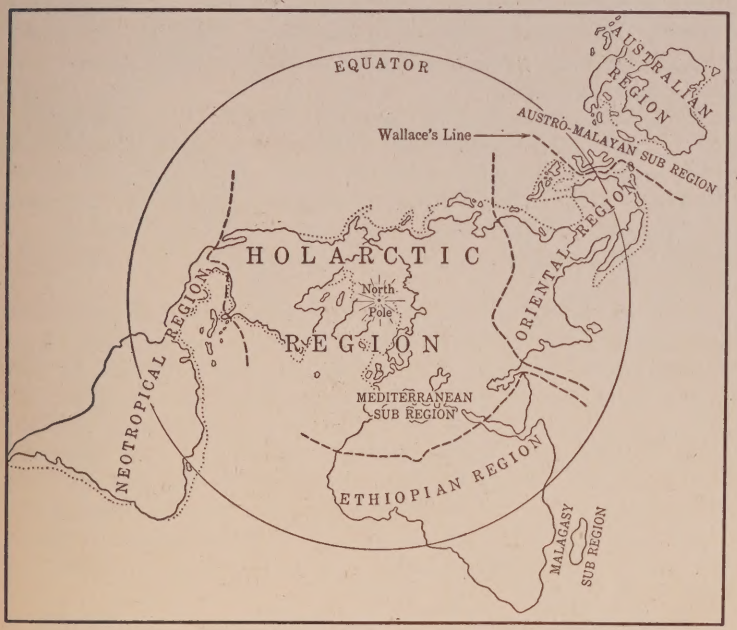

FIG. 147. — Map to show the principal realms of the earth as determined by their biological populations. Wallace's line marks and abrupt faunistic division between two neighboring geographical divisions. (After Matthew.)

Faunistic Areas. — A study of the faunas and floras of the world reveals the existence of great continental areas (Fig. 147) as shown on the accompanying map. These should be considered the resultant of the migration of organisms as limited by the competition with pre-existing species and the conditions of the climate. The modern study of animal and plant distribution (**Zoögeography** and **Phytogeography**) is based primarily on the evolution theory which it inspired. The existence of some species in widely scattered parts of the world has suggested the existence

of former land bridges in past geological periods, some of which have been demonstrated by the distribution of many different species. Thus ancient forms are often found only in regions remote from each other because they have been cut off by the incursions of new and better-adapted species. The ancient ganoid fishes which date back to the Devonian period are now found almost exclusively in the Mississippi basin, although they formerly were world wide in distribution. But the old world relatives have all disappeared except the Russian sturgeon and the Chinese spoonbill.

The differences in structure and distribution of modern species are best explained by the study of the structure and distribution of the species of the past geological period, and so on back to the Cambrian period, beyond which organic remains are few and far between. The comparison of these fossil floras and faunas period by period is the most convincing evidence of evolutionary change.

Many of the facts which have been ascertained about plants and animals in addition to those concerning the geological succession and geographic distribution are best explained by the theory of evolution. For this reason they are sometimes described as proofs of evolution. To the present writer this appears to stretch the meaning of the word proof. All that can be said is that the theory of evolution offers the best working hypothesis which the mind of man has yet devised to explain the facts which have been discovered, and that no body of evidence has yet been discovered which appears inconsistent with this hypothesis.

Comparative Morphology. — The classification of organisms is based on their similarities and dissimilarities. Similarities which apparently are due to genetic relationships, such as those between the bones in the arm of a man, the wing of a bat, and the flapper of a whale, are called **homologies,** even though changes have been effected through the use of the part for different functions. Similarities due to the use of different structures for the same function, when no genetic relationship exists, are called **analogies,** such as that existing between the wing of a bird and that of a butterfly. It is evident that two animals or plants closely related in evolution would have many homologous parts, while those distantly related but occupying comparable ecological positions might show analogous similarities. The evidence accords with the theory of evolution but does not prove it. For

example, the comparison of birds and reptiles suggests that they are closely related, and that the many similarities in their skeletons are homologous. No " missing link " survives today, but in the Triassic of Germany are found the fossil remains of *Archaeopteryx* (Fig. 148), a bird whose teeth, claws, and tail reveal it to be essentially a feathered reptile. So in botany the spermato-

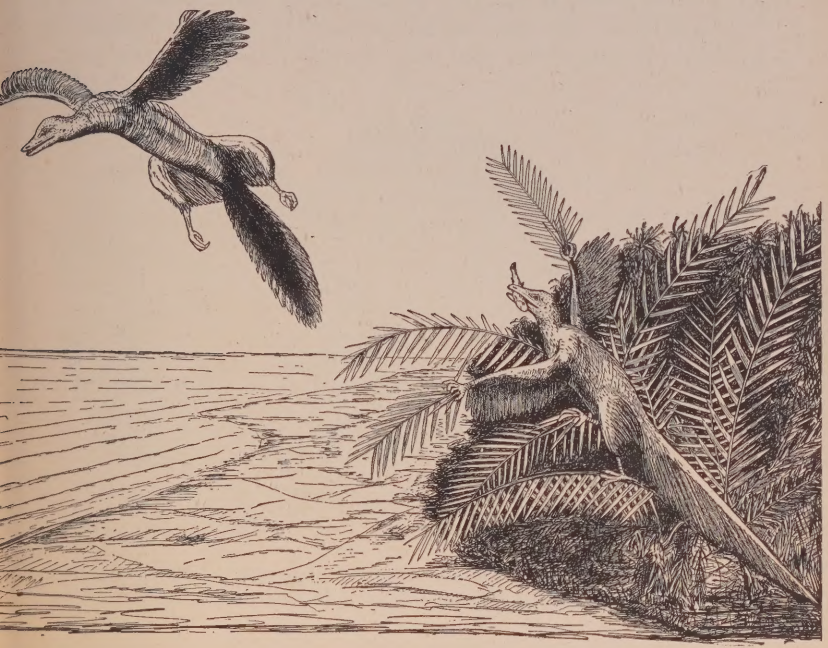

FIG. 148. — *Archaeopteryx*, the missing link between birds and reptiles, as restored by Berry. (From "Textbook of Palaeontology," The McGraw-Hill Book Co.)

phytes (or seed plants) are apparently descended from the pteridophytes (ferns and their allies), but no missing link exists in the flora of today. Yet among the fossils of the Jurassic are found the remains of Cycads (Fig. 149) which serve to bridge the gap.

The Recapitulation Theory. — The study of embryology has had its evolutionary period. Haeckel in 1866 propounded what he termed the biogenetic law, better known as the theory of

recapitulation, to the effect that every animal in its developmental history (**ontogeny**) recapitulates in an abbreviated and altered form the history of its race (**phylogeny**). The basis for this argument lay in the well-known facts that animals are more alike in the earlier stages of their development, and that the embryos of animals closely related to each other may resemble each other more closely than do the adults themselves.

It will be recalled that the larval stages of *Sacculina* (page 121) are the only evidence that this parasite is to be considered a

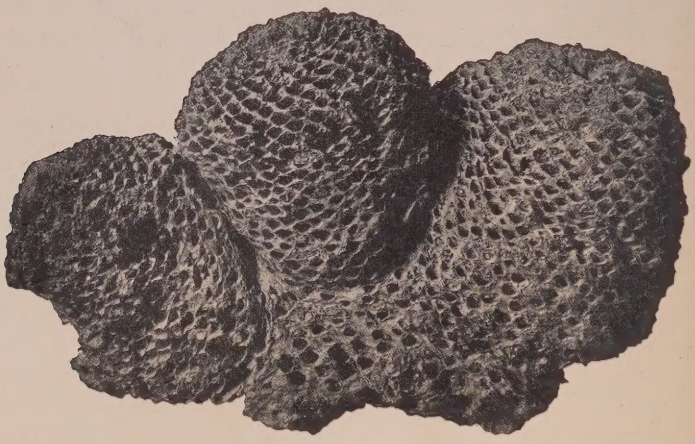

Fig. 149. — Fossil Cycads. The leaves of these plants were like those of the plant in the preceding figure. (From Pirsson and Schuchert.)

crustacean. The study of crustacean larvae by Müller in which he showed that the larvae of the higher crustacea resembled the adults of lower crustacea was the real origin of the recapitulation theory. The existence of vestigial organs is explained, on the basis of the recapitulation theory, by the supposition that these organs, e.g., the human vermiform appendix, once were useful adaptations and are preserved because the embryo recapitulated the ancestral stage in which the vestige had a functional importance.

Larval Adaptations. — It was recognized by the founder of this theory that the recapitulation must of necessity be very much abbreviated, for the organism has an infinitesimally short

life history as compared to the millions of years during which evolution has been going on. Furthermore, the conditions of embryonic and larval life as well as those of adult existence are affected by changes in the environment, so that many of the characters of the embryo must be considered larval adaptations (**coenogenetic** characters) rather than ancestral recapitulations (**palingenetic** characters). Thus the sucker by which the tadpole attaches itself to the egg jelly after hatching would

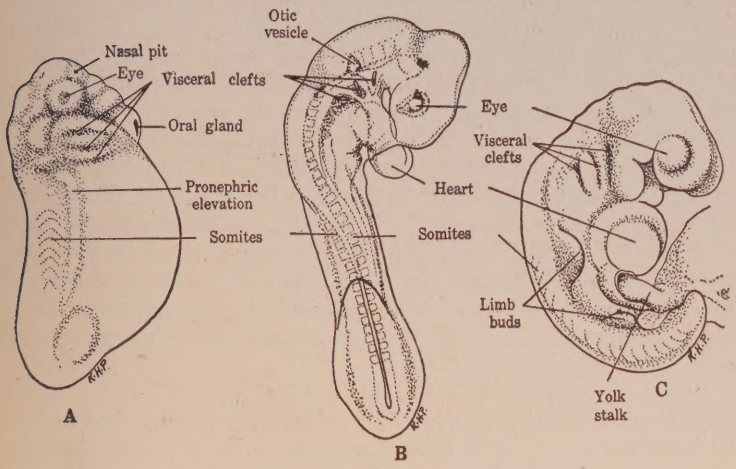

FIG. 150. — Early embryos of the frog, chick and man to show homologous structures. (After Patten, Kerr and His, from Shumway, "Vertebrate Embryology.")

hardly be considered an ancestral adaptation of some fish-like progenitor.

Modern Developments. — The development of genetics and experimental embryology has minimized the importance of this theory in modern Biology. The theory demands that each new stage in evolution be superimposed on the last in a serial order. But our knowledge of the gene indicates that a mutation affects the entire genetic complex, with the result that although the visible effect may not appear until late in ontogeny, the earlier developmental features are also altered. The effect of other genes may first become visible in the earliest stages of development although the mutation be the most recent to occur. So in

addition to the abbreviation of the record, and the interpolation of larval adaptations, the very order of the ontogenetic stages is no criterion of the evolutionary sequence.

Finally the very nature of development as an epigenetic process demands that each new stage in the development of the embryo and its parts be fashioned out of the material and structures so far developed. These are the architectural elements which will be remoulded and differentiated under the influence of the genes. Each such structure acts as an organizator for the reconstruction entailed by the next step in the developmental series. So the dorsal lip of the frog gastrula acts as an organizator to the whole process of germ-layer formation. Experimentally, the transfer of the dorsal lip region into another gastrula results in the organization of two embryos, one centering about each dorsal lip. On this hypothesis we should explain some vestigial organs such as the visceral pouches and grooves of the higher vertebrates, which correspond to the gill clefts of the fish, as organizators to the blood vessels, etc., which develop in that region. Many other so-called vestigial organs, such as the pituitary gland at the base of the brain and the pineal gland (once a median eye) at its roof, are now recognized as important endocrine glands whose secretions affect among other things the rate and limits of growth.

Summary. — Although the facts of classification, based on comparative morphology, and of embryology, also based on the comparison of structure, cannot be said to prove the existence of evolution, they fit the theory better than any other. It has often been shown that the facts of palaeontology, distribution, comparative anatomy, and comparative embryology all converge to show the close relationship between two groups of organisms. Therefore in the attempt to draw up genealogical trees showing the evolutionary history of plants and animals, all these facts must be taken into consideration, but with due respect to the weaknesses shown by each class of evidence. The imperfections of the geological record, which Darwin compared to a book, of which only a few pages were preserved and those badly mutilated; the difficulties of distinguishing ancient migration routes to account for the eccentricities of geographical distribution; the subjective factors involved in making distinctions between homologies and analogies; and the equally subjective task of distinguishing coenogenetic and palingenetic characters in ontogeny, combine to render the task of writing

evolutionary history one requiring "infinite resource and sagacity."

The present status of evolutionary relationships is expressed in the so-called natural system of classification which includes all known organisms both past and present. To the more important groups of plants and animals we shall now turn our attention.

CHAPTER X

THE PLANT KINGDOM[1]

The first great division of the plant kingdom includes all those plants which lack the root, stem, and leaves typical of the more highly organized plants. The group, known as the **Thallophyta,** includes the unicellular plants as well as some enormous and differentiated colonial seaweeds. It is the first to appear in geological history.

THALLOPHYTA

The thallophytes are a heterogeneous group and are divided into two subdivisions, the **Algae** and the **Fungi,** on the basis of their modes of nutrition, the algae including the holophytic forms which manufacture their food by photosynthesis and the fungi including the types which either manufacture their food by chemosynthesis (some bacteria) or are dependent upon other plants, the saprophytic bacteria, molds, etc.

The Algae. — The algae are water plants, although some few are found on the soil, rocks, stems of trees, etc., where they are exposed to moisture. They are typically green plants, although in some groups the pigment of the chlorophyll is obscured by red and brown pigments.

There are four classes of algae, the blue-green **Cyanophyceae,** green **Chlorophyceae,** brown **Phaeophyceae,** and red **Rhodophyceae.**

Cyanophyceae. — The blue-green algae are distinguished by the fact that they do not possess a formed nucleus, but contain scattered granules of chromatin, in the central area of the cell. Plastids too are absent, and the chlorophyll is found diffused in the outer region of the protoplasm, together with a blue pigment, and sometimes a red pigment, such as that found in a

[1] In this and the following chapter are given only the barest outlines of the plant and animal kingdoms, so that the reader may have some idea of the diversity of types produced by organic evolution. For further information, textbooks of general botany and general zoölogy should be consulted.

blue-green alga[2] which gives its name to the Red Sea. The cell wall generally is composed not of cellulose but **chitin,** a nitrogenous compound found also in bacteria and many animals. Another peculiarity of these plants lies in the fact that they secrete a jelly-like substance which forms a matrix binding the daughter cells together in a sort of colony. Instead of forming starch, the blue-greens manufacture glycogen, like the fungi

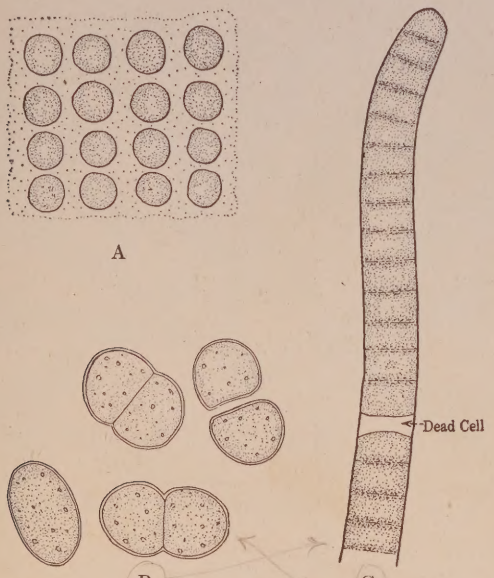

FIG. 151. — Cyanophyceae, blue-green algae. A, *Merismopedia,* a plate-like colony; B, *Oscillatoria,* a filamentous colony; C, *Synechococcus,* a solitary species. (From Holman and Robbins.)

and many animals. These algae reproduce by division, and no sexual reproduction has been observed. They form an important element in the plankton of marine and fresh waters, and can endure high temperatures and a degree of pollution beyond that tolerated by other algae. Both unicellular and colonial types are found.

Chlorophyceae. — The green algae have only the normal pigments associated with chlorophyll, and these are located in

[2] *Trichodesmium erythraeum.*

plastids. A definite nucleus is present, and the cell wall is formed from cellulose. Starch is manufactured by most of the green algae. They reproduce by division and in many cases, e.g., *Oedogonium* (Fig. 101), by syngamy. They are found mostly in fresh-water plankton, although some, the **diatoms** (Fig. 152 *D*), are also found in the marine plankton of tropical seas. They cannot endure as much heat or pollution as the blue-greens. A

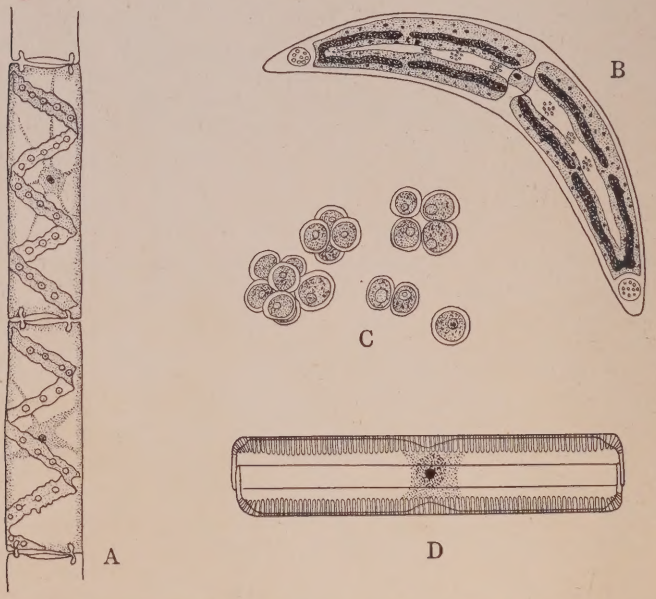

FIG. 152. — Chlorophyceae, green algae. A, *Spirogyra*, a filamentous colony; B, *Closterium*, a desmid; C, *Protococcus*, a solitary form; D, *Navicula*, a diatom. (After Conn, except D, after Ehrenburg.)

few are found in moist soil or upon the moist surface of trees, etc. The algal component of lichens is usually a green alga, but sometimes a blue-green occupies this position. Some green algae are found symbiotic in the bodies of coelenterates (green *Hydra*) and flatworms. Among the interesting groups are the desmids (Fig. 152 *B*), which are characterized by the fact that the cell body is constricted into two halves, with the nucleus situated in an isthmus between them. The cell wall of the diatoms is impregnated by silica to form an exoskele-

ton of two valves, often beautifully sculptured. They are well known to microscopists as test objects by means of which the resolving power of the microscope may be determined. These valves persist after the death of the organism and accumulate at the bottom of lakes or the sea to form layers of diatomaceous earth, useful in polishing and the manufacture of dynamite. Many of the green algae, *Volvox* (Fig. 71) for example, lie on

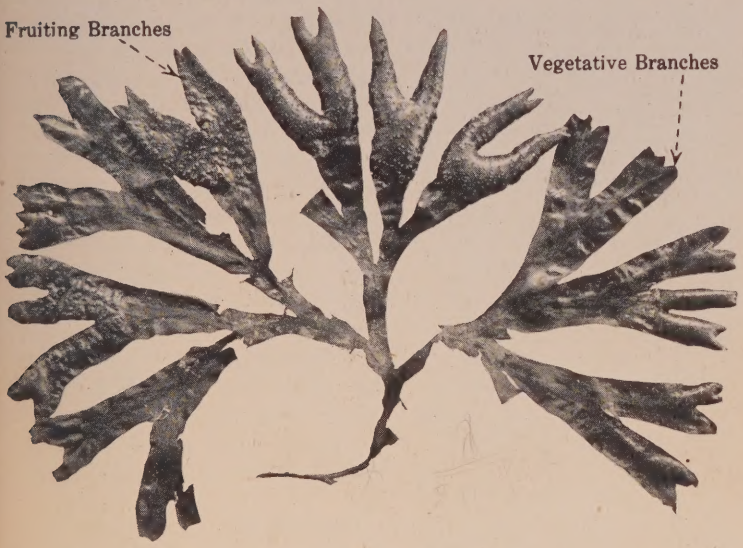

FIG. 153. — *Fucus*, one of the Phaeophyceae or brown algae. One of the common seaweeds. (From Holman and Robbins.)

the boundary line between the plant and animal kingdoms and may equally well be classified as flagellate animals.

Phaeophyceae. — The brown algae include some microscopic forms but are best known as the seaweed and kelp of the sea. Practically all are marine. They form the major part of the benthos of the sea, as they grow attached to the bottom, developing root-like holdfasts. A few normally grow detached as floating forms, such as *Sargassum*, which forms the great bed of vegetation in the Sargasso Sea of the North Atlantic ocean. These have air bladders arising from the accumulation of gases between the cells in certain localities. In many of the kelp there is an alternation of generations between an asexual phase pro-

ducing zoöspores, and a sexual phase which produces megagametes and microgametes. In the true seaweed or bladder-wrack, *Fucus* (Fig. 153), reduction takes place just prior to fertilization as in animals. No asexual spores are formed by *Fucus*.

Rhodophyceae. — The red algae (Fig. 154) contain a red pigment in addition to those characteristic of chlorophyll. Starch is not formed, but another polysaccharose is manufactured instead. In some groups the cell walls become impregnated with carbonate of lime like the corals and play an important rôle in the building of coral reefs. They are found in the greatest abundance in tropical water and occupy the deeper zones of the littoral waters. The red algae are able to grow at greater depths than the green or brown algae, and are always found as colonies. An alternation of generations takes place, and the reduction division is delayed until the plant body has attained considerable size.

Fig. 154. — *Pterosiphonia*, one of the Rhodophyceae or red algae. (From Holman and Robbins.)

Organization of the Algae. — Even the giant kelps, some of which attain a length of 200 meters, do not have the organization of the higher plants. As they are supported in the water, and surrounded by it, they need no supporting and conducting tissues, nor special organs for absorption and photosynthesis. The principal differentiation is that necessary for purposes of reproduction.

The algae probably represent a number of different evolutionary lines, which like the primitive animals seem to originate from the flagellates, on the boundary between animals and plants. Representing various types of adaptation to aquatic communities, they form the primary source of food for the animal life of the sea and the fresh waters.

The Fungi. — Like the algae, the fungi form a heterogeneous group. It contains the parasitic and saprophytic plants, with the exception of those clearly related to more highly organized groups. Five classes are distinguished: the **Schizomycetes** or bacteria, the **Myxomycetes** or slime fungi, the **Phycomycetes** or algal fungi, the **Ascomycetes** or ascus fungi, and the **Basidiomycetes** or basidium fungi.

FIG. 155. — Coccus forms of bacteria. A, *Staphyloccus;* B, *Diplococcus;* C, *Streptococcus,* D, *Sarcina.* ×1000. (From Holman and Robbins.)

Schizomycetes. — The bacteria are microscopic unicellular plants, which are sometimes united in irregular masses or threads. The cell wall contains no cellulose but is sometimes surrounded by a gelatinous matrix which holds the cells together. There is no nucleus, but chromatin granules are distributed thoroughout the cell. Nutrition is parasitic or saprophytic, with the exception of the chemosynthetic forms noted previously. The distribution of the bacteria is universal, and their remains have been found in the oldest rocks. They are found in the atmosphere, on the surface of the earth, in deep borings, in all waters fresh and marine, and on all moist surfaces of animals and plants. Parasitic forms have been found in practically every tissue of the plant and animal body. There are three morphological types of bacteria: **cocci** (Fig. 155) or spherical forms, **bacilli** (Fig. 156) or rod-like forms, and **spirilla** (Fig. 157) or spiral forms. The bacteria reproduce entirely by division, and there is no evidence of a sexual stage. The cell wall thickens in spore formation so that the cell is able to resist desiccation, high temperatures, the action of poisons (disinfectants), etc. The anthrax organism,[3] is killed after a two-minute treatment with 1 per cent carbolic acid, but the

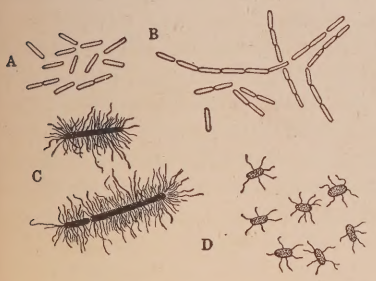

FIG. 156. — Bacillus forms of bacteria. A, *Bacillus sporogenes;* B, *B. subtilis;* C, *B. proteus;* D, *B. typhosus.* ×750. (From Holman and Robbins.)

[3] *Bacillus anthracis.*

spores will remain alive for as long as fifteen days in the same solution. The spore escapes from its wall (germination), which softens under favorable conditions, and forms a new cell wall to continue existence as a vegetative cell. The process may be compared with encystment in other unicellular organisms.

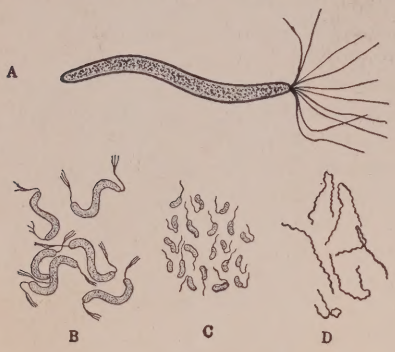

Fig. 157. — Spirillum forms of bacteria. A, *Thiospirillum;* B, *Spirillum undulum;* C, *Vibrio cholerae;* D, *Spirochaeta.* ×1000. (From Holman and Robbins.)

The bacteria may well have been the first form of life upon the earth, but there is no evidence of any evolutionary connection between these fungi and the simplest flagellates. With regard to the origin of the bacteria themselves, it has been suggested that their spores might have been carried to the earth on cosmic dust from other astronomical bodies, surviving in spite of the extremely low temperatures of interstellar space. A recent suggestion, however, is that they may have been derived from the so-called ultra-microscopic **viruses.**

Ultra-Microscopic Viruses. — These viruses, sometimes known as filterable viruses, are fluids extracted from diseased organisms. They will pass through porcelain filters whose pores are too small to permit the passage of visible particles. The introduction of the virus into the body of another individual will cause the same disease. It is believed from the behavior of these viruses that they contain ultra-microscopic organisms which have the power of growth and reproduction and secrete toxins as a by-product of their metabolism. Whether these organisms should be considered infinitesimal bacteria or some simpler form of life is not clear. There has been suggested recently the possibility that they might be considered independent genes and so represent the first stage in the evolution of life. For the present, at least, this can be considered only an interesting hypothesis.

Myxomycetes. — The Myxomycetes (Fig. 158) like the flagellates have both plant and animal characteristics, and zoölogists often include them among the protozoa as Mycetozoa. In their

vegetative stage, these organisms are multinucleate masses of naked protoplasm which form pseudopodia like *Amoeba* and have a holozoic mode of nutrition. In reproduction, however, they develop structures called **sporangia,** which produce the spores. These possess cellulose walls. When the sporangium wall dries

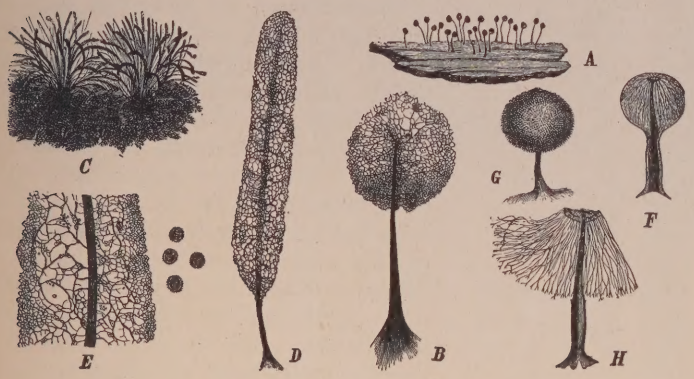

FIG. 158. — Myxomycetes or slime-molds. Also claimed by the zoölogists under the name Mycetozoa. A–B, *Comatricha negra;* C–E, *Stemonitis fusca;* F–H, *Enerthema papillatum.* (From Harshberger, from Holman and Robbins.)

and breaks, the spores are scattered, to germinate if they fall in water. The spore wall is ruptured and the naked cell develops a flagellum and swims about as a swarm-spore, multiplying by division. Finally the flagellum is resorbed, the spore takes on an amoeboid form and at last unites with others to form the plasmodium. There is no sexual stage unless the formation of the plasmodium can be considered in this light. Nothing is known as to the existence of reduction.

Phycomycetes. — The Phycomycetes include the molds, and resemble the filamentous algae in the absence of cross walls in their filaments (**hyphae**). *Saprolegnia* (Figs. 159, 160), an example of this class, is found in ponds and streams on the decaying bodies of dead animals. A few species attack young fish and their eggs. The body of the plant is composed of branched filaments, each of which contains a series of nuclei, but the cytoplasm is not divided by cross walls into separate cells. In the vegetative stage these absorb organic material from the bodies on which they live. They reproduce asexually by forming spo-

rangia (Fig. 159) which are the swollen terminal portions of hyphae and are separated from the rest of the filament by a cross wall. In the sporangium are formed a number of flagellated zoöspores, which swim about until they settle down and give rise to new hyphae. If a new source of food material is not encountered soon, the zoöspores may encyst for a time before continuing the search. Sexual reproduction is initiated by the appearance of **oögonia**, which form large immobile eggs; on other hyphae sperm-producing **antheridia** develop. These curve about until they come in contact with the oögonia, when they send out slender tubes each containing a few non-motile microgametes. These penetrate the wall of the oögonium, pierce the eggs and bring about fertilization. The fertilized eggs give rise to new hyphae. Even if fertilization does not take place, the egg develops parthenogenetically. The bread mold, downy mildews, and many other forms, many of which cause diseases in both plants and animals, are found in this group.

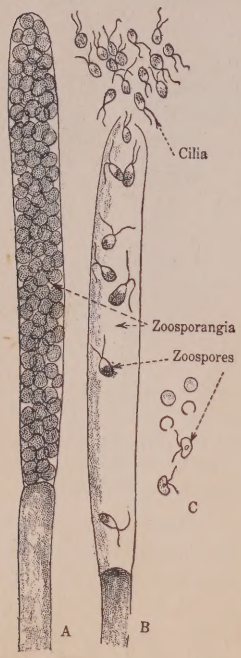

FIG. 159. — *Saprolegnia*, or water mold, one of the Phycomycetes. Asexual reproduction by zoösporangia. (From Holman and Robbins.)

Ascomycetes. — The Ascomycetes are the largest group of fungi. They are called the ascus fungi because they develop sac-like hyphae in which the powdery and non-motile spores are formed. The hyphae have cross partitions (**septae**). Many parasitic forms causing rots, powdery mildews, and other plant diseases are found in this group. Some, including the blue and green molds, are saprophytic. The yeasts are usually included in this group because, when well oxygenated, the nucleus divides two or three times to form four or eight **ascospores** (Fig. 93). The lichen fungus (Fig. 161) is generally one of the Ascomycetes. The group shows some resemblances to the brown algae from which they may have originated.

Basidiomycetes. — The Basidiomycetes are distinguished by the formation of a **basidium** or club-shaped hypha which gives rise to the spores. In this group we find the smut fungi which

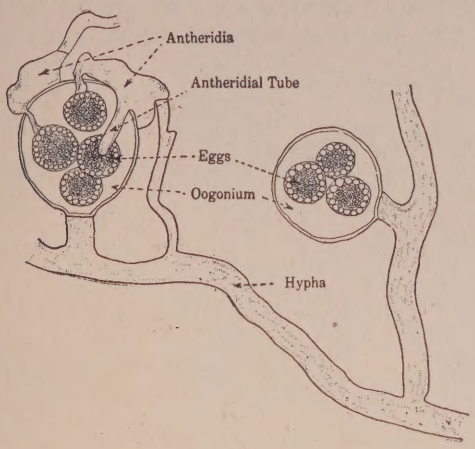

Fig. 160. — *Saprolegnia.* Sexual reproduction by antheridia and oögonia. (After Sinnott, from Holman and Robbins.)

cause great economic losses because they are parasitic on the grasses. The rust fungi often pass through an alternation of generations involving two different hosts, such as the white pine and the currant, or the grasses and the barberry. The more familiar mushrooms and puff-balls are also included in this group. The mushroom is only the fruiting body or reproductive organ. The real body of the plant is the saprophytic **mycelium** composed of a mesh of hyphae. From a mass of interwoven hyphae beneath the surface arises a stalk crowned with an umbrella-like cap on

Fig. 161. — A lichen or fungus-alga complex. The fungus element probably belongs to the Ascomycetes. (From Holman and Robbins.)

the underside of which are numerous radiating plates called the **gills** which bear the basidia. A single **sporophore,** as the fruiting body is called, of the cultivated edible mushroom[4] will liberate 1,800,000,000 spores which are distributed by air currents (Fig. 162). The Basidiomycetes reproduce entirely asexually,

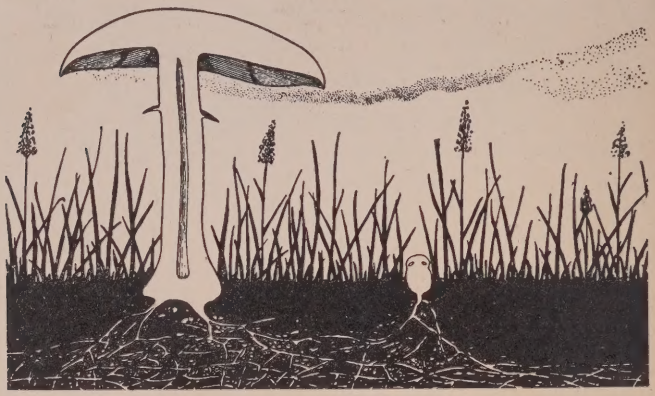

FIG. 162. — Diagram of *Psalliota arvensis,* the horse-mushroom, one of the Basidiomycetes. Note the air-borne cloud of spores. $\times\frac{1}{2}$. (From Buller, from Holman and Robbins.)

with the exception of the rusts, in which sexual reproduction is known. It is believed that they originated from the Ascomycetes.

BRYOPHYTA

The Bryophyta are terrestrial plants, although for the completion of their life cycle they require a moist season. An alternation of sexual and asexual generations always occurs. The asexual plant (sporophyte) is smaller than the sexual plant (gametophyte) and is permanently attached to the latter, upon which it grows parasitically. This is the reverse of the conditions which we find in the higher plants. The epidermis of the bryophyte is adapted to terrestrial conditions, as its cells are provided with a cuticle. No roots are formed, their place being taken by the **rhizoids** of the gametophyte. The archegonium forms a single megagamete, while the antheridia give rise to many

[4] *Agaricus campestris.*

biflagellate sperm. These swim to the archegonium, which they enter, and one fertilizes the egg. In the simplest type (*Riccia*) (Fig. 163), this gives rise to the diploid sporophyte which remains

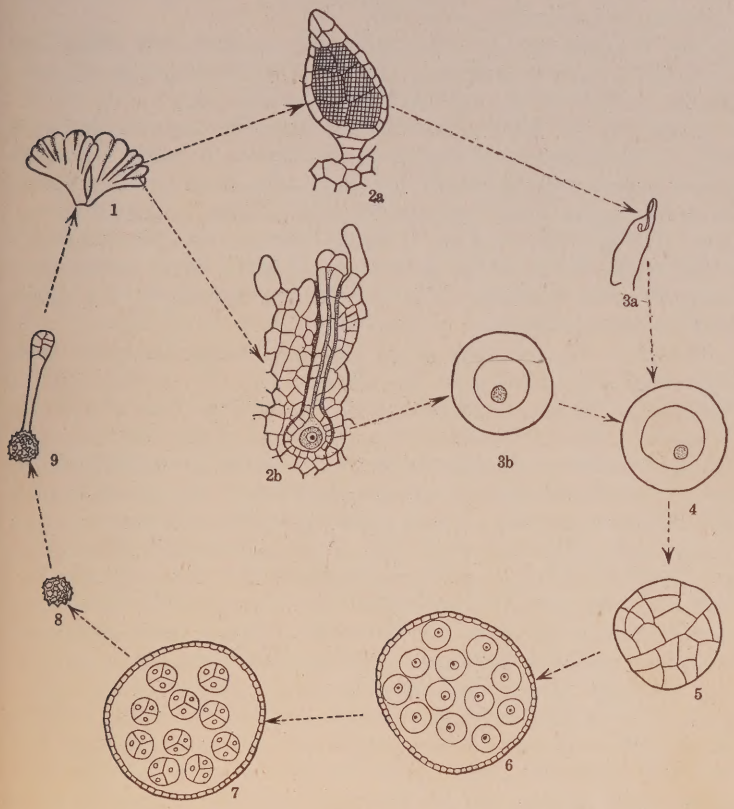

FIG. 163. — Diagram to show life history of *Riccia*, one of the Bryophyta. 1, gametophyte thallus; 2a, antheridium; 2b, archegonium; 3a, sperm; 3b, egg; 4, zygote; 5, embryo sporophyte after cleavage; 6, sporophyte with spore mother cells; 7, same after maturation divisions; 8, spore; 9, embryo gametophyte. (From Holman and Robbins.)

within the cavity of the archegonium. The sporophyte consists of an outer wall of flattened cells containing a number of free spherical spore mother cells, each of which later undergoes two

maturation divisions and gives rise to four haploid spores. These are freed when the gametophyte dies and later germinate to form new gametophytes. It must be remembered that in the bryophytes the gametophyte generation is always haploid while the sporophyte generation is diploid.

The bryophytes are divided into two groups, the **Hepaticae,** liverworts, and the **Musci,** mosses. Representatives of these groups are among the earliest known land floras.

Hepaticae. — The liverworts are sometimes thallose, that is to say, without leaves or roots. Some, however, have a gametophyte generation in which the body has a stem with simple close-set leaves. The sporophyte often shows more differentiation, and may have a **foot,** or organ by which the plant attaches itself to the tissue of the gametophyte, and a **stalk** communicating with the **capsule.** The capsule corresponds to the sporophyte body of *Riccia.*

Musci. — The mosses (Fig. 100) are better adapted to a terrestrial existence than the liverworts. Some are aquatic, many grow on the soil and some on rocks and the bark of living or decaying trees. The gametophyte consists of a green branching filament known as the **protonema,** which sends up the leafy shoots called the **gametophores.** From the base of the gametophores the rhizoids grow out, branch, and sometimes give rise to a new protonema. The epidermal cells of the gametophore are cuticular, and the internal cells are elongated for water conduction. Some shoots give rise to antheridia, about which the leaves expand to form a flower-like structure. Others form archegonia with long necks, down which the biflagellate sperm swim to fertilize the egg. The zygote develops in the cavity of the archegonium until mature, when it bursts out as a sporophyte with a foot, stalk, and capsule like those of the liverworts, except that comparatively few cells of the capsule are spore mother cells. Each spore mother cell by means of two maturation divisions produces four haploid spores from which the gametophytes germinate. The sphagnum mosses of peat-bogs differ from the others in that the protonema is a thallus rather than a network of filaments, and the leaves contain large empty cells with apertures which give the dry moss its absorptive power.

Organization of the Bryophyta. — All bryophytes are imperfectly adapted to a terrestrial existence because their rhizoids cannot penetrate the soil to any great extent. The lack of supporting tissues will not permit them to grow erect to any

height. The possession of flagellate sperm requires a rainy season, as fertilization can take place only when the gametophyte is wet.

PTERIDOPHYTA

In the Pteridophyta (fern-like plants) we note a greater adaptation to terrestrial conditions. This group includes the **Filicineae** or true ferns, the **Equisitineae** or horsetails, and the **Lycopodineae** or club mosses. These plants have flagellated sperm and so require a rainy season to insure fertilization. The archegonia and antheridia also are of the bryophyte type. In this group, however, the sporophyte is better developed and dependent upon the gametophyte for only a short period. The sporophyte develops root, stem and leaves, while the gametophyte is still an independent thallus plant much like a liverwort. The pteridophytes were the dominant land plants of the Palaeozoic Age, and included large tree-ferns.

Filicineae. — The common fern (*Polypodium*), (Fig. 164) is in the sporophyte generation, with a subterranean stem (**rhizome**) from which the adventitious roots descend and the leaves (**fronds**) arise. These fronds are **sporophylls** (spore leaves) from which the haploid spores are discharged. The germinating spore produces a monoecious gametophyte with archegonia and antheridia much like those of the bryophyte. The sperm swim to the archegonium and fertilize the egg. This gives rise to the diploid embryo sporophyte. This generation develops a connecting foot like that of the bryophyte by which it derives its food from the tissues of the gametophyte. Later a primary root, stem, and leaf develop. The primary root and leaf are embryonic organs later replaced by the adventitious roots and fronds. The roots are provided with a root cap, root hairs, and a single vascular bundle. The stem has an epidermis, parenchyma, and a number of vascular bundles each surrounded by an endodermis. The vascular bundles have no cambium, and the phloem surrounds the xylem. The fronds have a stalk which continues into a midrib (**rachis**) from which the leaflets branch out on either side. The structure of the leaf is like that of the seed plant. Most ferns are homosporous, that is, there is no distinction between male and female gametophytes, but in the water ferns and some of the extinct races, some sporophylls give rise to megaspores from which female gametophytes develop, and others form microspores from which male gametophytes arise.

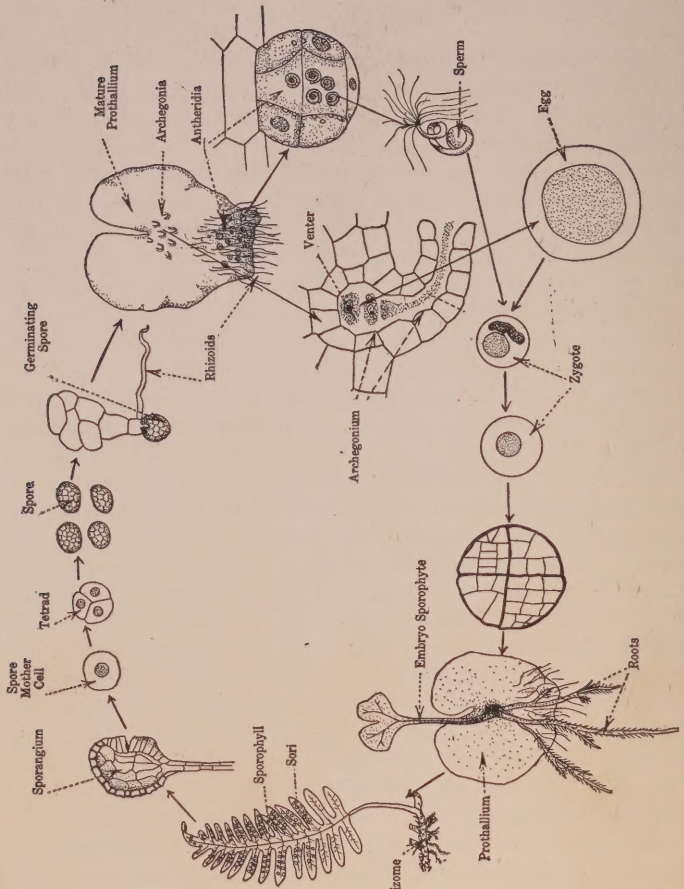

FIG. 164. — Diagram to show life history of fern, *Polypodium*. See text for explanation. (From Holman and Robbins.)

Equisitineae. — The horsetails are represented today by only thirty species of a single genus (*Equisetum*) (Fig. 165), but in the Palaeozoic this class was a dominant in many conmunities. While one of the tropical species is a slender plant climbing with the aid of others to a height of thirty feet, most of the modern species are very small. But in the fossil remains we find horsetails of truly tree-like dimensions and with woody stems (*Calamites*)

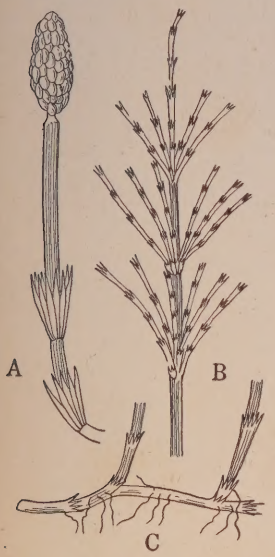

FIG. 165. — The Horsetail, *Equisetum*. Sporophyte generation. A, spore-bearing shoot; B, vegetative shoot; C, rhizome. $\times\frac{2}{3}$. (After Britton and Brown.)

FIG. 166. — *Selaginella selaginoides*, one of the club-mosses or Lycopodineae. One of the creeping species. Natural size. (After Britton and Brown.)

(Fig. 167). Some of these extinct horsetails were heterosporous and therefore developed both male and female gametophytes. The outer layers of the sporophyte are impregnated with silica, which stiffens the stem. The stem leaves are reduced to mere scales. The internodes of the stem are hollow like a grass. The spore leaves are grouped at the tip of the stem into a cone-like **strobilus.** The modern *Equisetum* is homosporous. The archegonia and antheridia of the gametophyte are in such close association that the multiflagellate sperm swims to the egg and

FIG. 167. — Restoration of a Pennsylvanian landscape. Note *Calamites*, and pteridosperms in foreground, *Sigillaria* and tree-ferns in mid-distance. Three species of extinct amphibians are shown. (From Knipe, from Pirsson and Schuchert.)

FIG. 168. — Restoration of a Pennsylvanian swamp to show *Lepidodendron* and tree-ferns in foreground, pteridosperms in mid-distance. (After Unger, from Pirsson and Schuchert.)

fertilizes it, after which development takes place much as in the fern.

Lycopodineae. — The club mosses include about six hundred living species, mostly tropical, of two genera (*Lycopodium* and *Selaginella*), but like the horsetails, they played a more important part in past geological periods. In the later Palaeozoic, some of the extinct forms gave rise to tree-like woody plants with a height of nearly a hundred feet (*Lepidodendron*) (Fig. 168). *Selaginella* (Fig. 166), a modern creeping plant, has an aerial stem (runner) with root-like **rhizophores** which act as supports but may develop roots if they touch the soil. Sterile leaves and spore leaves are differentiated, the latter of which are grouped in strobili containing both megasporophylls and microsporophylls.

SPERMATOPHYTA

The Spermatophyta or seed plants are the dominant plants of modern times. Although they are typically terrestrial plants, some species are found in the littoral zone of the sea, and the shallower stretches of fresh waters, but not in the deeper waters. They represent a great advance over all the divisions heretofore considered in their adaptation to the terrestrial habit. The development of the pollen tube and the disappearance of the flagellated sperm (in all save a few of the more primitive species) permit fertilization without the presence of water. The production of seeds favors a wider distribution and allows the plant to weather unfavorable seasons with extremes of temperature and humidity. The all-but-disappearance of the gametophyte generation and the development of mechanical and conducting tissues increase the size and efficiency of the sporophyte generation. There are two classes of Spermatophyta, the **Gymnospermae** (naked-seeded plants) and the **Angiospermae** (covered-seeded plants).

Gymnospermae. — The Gymnosperms include the evergreen conifers, the cycads, ginkgos, and gnetals. These forms dominated the Mesozoic Age but at the present time include only about 500 species. The cycads were a more important group in the Mesozoic and seem to have descended from a race of seed-bearing ferns (**Pteridospermae**) of the Palaeozoic, which did not survive into Mesozoic times.

Coniferales. — The Coniferales include the pines, spruces, firs, larches, junipers, Douglas fir, redwood, and big tree. The

pine tree is the sporophyte generation. The shoot is distinguished by its cone-shaped system with a single axis and many lateral branches. The needle-like leaves are in bundles of two to five, and are retained over the winter. The stem is woody with a well-developed bark, but no tracheal tubes are found in the xylem, their place being taken by single conducting cells, **tracheids.** The spore leaves or sporophylls are borne in cones, and two types of cone, megasporangiate (carpellate) and microsporangiate (staminate), are found on the same tree. The megasporangiate cones are the familiar pine cones and consist of a central axis around which the megasporophylls are arranged in spiral fashion. Each leaf is composed of a short stalk, bract, and ovuliferous scale. Each scale bears on the upper side near its base two megasporangia or ovules. The ovule consists of a nucellus with a single integumentary layer and a micropyle which is directed towards the stalk. The microsporangiate cones are smaller and found in groups at the ends of some of the branches. The cone is like the megasporangiate type except for its size and the fact that its sporangia are pollen sacs.

The Life Cycle of the Pine. — In the nucellus or megasporangium a single large megaspore mother cell undergoes two maturation divisions to form a linear group of four megaspores, with haploid nuclei. The one farthest from the micropyle enlarges at the expense of the other three. In the pollen sac or microsporangium many microspore mother cells give rise to haploid microspores following the two maturation divisions. Each spore has two wing-like extensions formed by the separation of exine and intine and filled with air, by means of which it is carried great distances at the time of pollination. Within the spore walls, the nucleus divides twice. One nucleus degenerates at each division. These are the first and second vegetative nuclei corresponding to the vegetative cells of the ferns. The nucleus remaining together with the surrounding cytoplasm represents the antheridium. This cell divides to form a generative cell and a tube cell. The pollen (microspores) which reaches the megasporangiate cones sifts down upon the ovules which secrete a sticky fluid to which the pollen adheres. As the fluid dries, the pollen is drawn, by capillary attraction, through the micropyle and up to the nucellus. Soon after pollination the leaves of the cone grow into contact with each other and are sealed with pitch while the stem curves to invert the cone. The pollen wall is ruptured and a pollen tube grows into the nucellus, sometimes developing

branches by which it obtains its food from the tissue of the nucellus like a parasite. This growth ceases during the winter but is resumed the following spring.

At this time the megaspore divides a number of times to form the female gametophyte, sometimes called the endosperm. Later in the spring, at the micropylar end of the endosperm, two or three surface cells enlarge, and each develops into an archegonium, with eight small neck cells, a large egg cell and a ventral canal cell which soon disappears. The pollen tube meantime has grown down to the endosperm, and its generative cell divides into a stalk cell and a body cell. The nucleus of the body cell divides to form two sperm nuclei, each of which has a body of cytoplasm but no cell wall. On reaching the endosperm, which is the female gametophyte, the pollen tube or male gametophyte destroys the neck cells and discharges all four of its nuclei into the egg. One of the sperm nuclei conjugates with the egg nucleus to form a zygote nucleus, while all the others disintegrate.

The zygote forms the embryo by dividing four times to form four layers of four cells each, of which the uppermost layer is not cut off from the remaining cytoplasm of the egg. The lowest layer contains the embryonic cells; the next contains suspensor cells, by whose elongation (at the expense of the two upper layers and the remaining cytoplasm) the embryo is driven deeper into the endosperm. Each embryo cell may give rise to an embryo, but one outstrips the others to become the functional embryo of the seed. The endosperm grows at the expense of the nucellus, and the embryo at the expense of the endosperm. The embryo develops a primary root (radicle), shoot (hypocotyl), and three to eight leaves (cotyledons). After the seeds have matured, the leaves of the cone dry, separate, and allow the seed to fall. If conditions are favorable they germinate to give rise to new sporophytes. In the pine more than a year passes between pollination and fertilization, and the seeds preserve their vitality for long periods.

Other Gymnosperms. — The **Cycadales** extend far back into geological time. They are dioecious, that is to say, the sporophyte possesses either microsporophylls or megasporophylls, but not both. The ginkgo or maidenhair tree is another survivor of an ancient race. It has sterile fan-shaped leaves and is dioecious. It is curious to note that this race was perpetuated in historical times only because of its use as an ornamental tree in Chinese cemeteries, and has never been found elsewhere. In both these

orders the pollen tubes produce motile sperm which are discharged when the tube nears the end of the female gametophyte so that the sperm swim a short distance before entering the egg. This seems a last reminiscence of the aquatic origin of the plants. The remaining order of the **Gnetales** includes some trees with tracheal tubes and an embryo-sac like that of the angiosperms.

Angiospermae. — The angiosperms with over 130,000 species are the largest group of plants and the dominant race of today. They first appear in the Cretaceous period and from that time on are the predominating element in every land flora. They are distinguished from the gymnosperms by the fact that the seed develop inside a closed ovary formed by the fusion of one or more megasporophylls (carpels). Both woody and herbaceous plants are found. Some are annual like the wheat, some biennial like the beet, others perennial like the hardwoods. The xylem has tracheal tubes. Megasporophylls, microsporophylls, and sterile leaves unite to form a flower, on account of which the angiosperms are often called the flowering plants. The ovary and some other parts of the flower with the contained seed form a fruit. The male gametophyte or pollen tube has but three cells, whereas that of the gymnosperms has six. The female gametophyte or embryo-sac has only a few cells, whereas that of the gymnosperm has thousands. The endosperm is formed after fertilization by the union of a haploid sperm nucleus with two haploid polar nuclei so that its cells are triploid. In the gymnosperm the female gametophyte arising directly from the megaspore is the endosperm, and its cells are therefore haploid.

The life cycle of the wheat as described in Chapter III serves to illustrate the life cycle of an angiosperm. Two classes of angiosperms are distinguished, the **Dicotyledones** and the **Monocotyledones.** The dicots have two cotyledons in the embryo, as in the bean, whereas the monocots have a single cotyledon, as in wheat. The leaves of dicots have an open venation with the veinlets branching and interlacing in all directions. In the monocot the venation is closed and the veins are parallel.

The stem of the dicot has a vascular ring, containing cambium. Thus the xylem and phloem grow concentrically so that the size of the stem increases at the base and tapers upward. The vascular bundles of the monocot are scattered and possess no cambium, so there can be relatively little growth in thickness. The root of the dicot generally has a taproot, developed by the growth of the primary root, while the monocot develops adventitious roots from

the lower part of the stem. The flower of the dicot usually has cycles of five or four flower parts (modified sporophytes). The flower of the monocot usually has cycles of three.

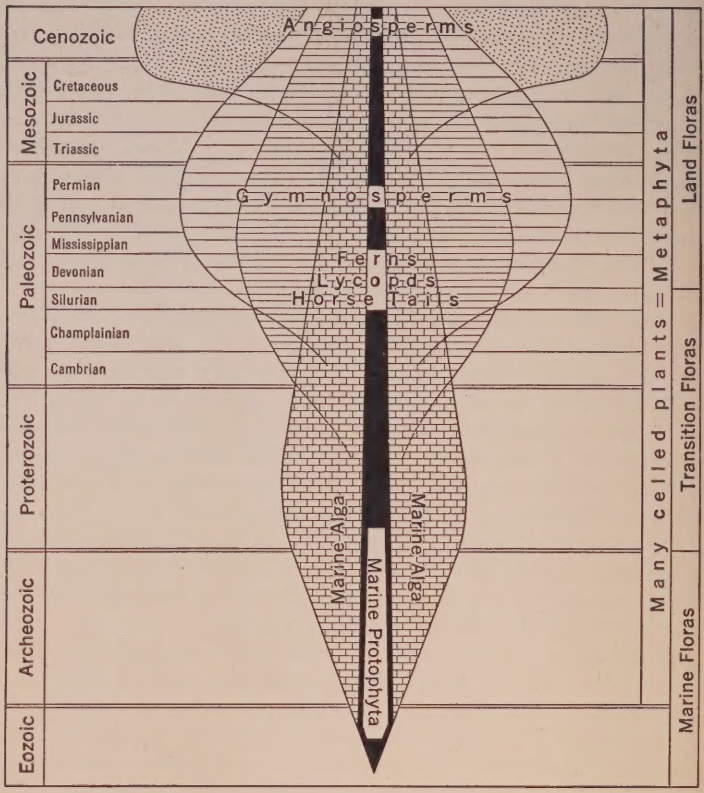

FIG. 169. — Diagram to show the probable course of evolution in the plant kingdom. The lines bounding each group expand and contract according to the growth in the number of species. (After Berry, from Pirsson and Schuchert.)

Summary. — The evolution of the plants (Fig. 169) shows a slow succession from unicellular aquatic plants to multicellular thallus plants which may be aquatic, saprophytic or parasitic. The first terrestrial plants, the bryophytes, have an alternation of generations between a sexual, haploid, holophytic gametophyte

and an asexual, diploid, parasitic sporophyte. In the next stage, seen in the pteridophytes, the gametophyte, while still an independent holophytic plant, is reduced in size and importance, whereas the sporophyte, after a temporary parasitic existence within the archegonium of the gametophyte, soon becomes independent and holophytic. The seed-plants are distinguished by the reduction of the sexual generation to the parasitic male gametophyte and the equally parasitic female gametophyte, by the loss of motile sperm, and by the development of seed. The culmination of plant evolution is found in the flowering plants, in which the male gametophyte or pollen tube is even more rudimentary and the female gametophyte is reduced to the embryo-sac. The monocots, especially the grasses, show a tendency towards a monoecious sporophyte generation that is, a segregation of microsporophylls from megasporophylls.

CHAPTER XI

THE ANIMAL KINGDOM

The animal kingdom, because animals have the power of locomotion and a diversity of food habits, includes a wider range of species than does the plant kingdom. There are three times as many species of animals as there are of plants. These are arranged in phyla, but there is no general agreement among zoölogists as to the number of phyla or the allocation of some groups of animals to them. It may be said, however, that there are at least ten well-marked phyla, with about as many groups whose position is uncertain.

PROTOZOA

The first phylum is that of the Protozoa. This includes all the unicellular animals, whether they are independent cells or form colonial aggregates. Here belong *Euglena*, *Amoeba*, and *Paramecium* already mentioned in earlier chapters. Because certain groups, like the Phytoflagellata and the Myxomycetes, might properly be placed either among the Thallophyta or the Protozoa, some writers have proposed the term **Protista** to include the unicellular algae and fungi (Protophyta) as well as the Protozoa in a separate kingdom. The Protozoa include the **Flagellata, Sarcodina, Ciliata, and Sporozoa.**

Flagellata. — The Flagellata are distinguished from the others because they move by the lashings of a microscopic whip, the flagellum. They reproduce by division. Among them are found forms which have the holophytic method of nutrition, the saprophytic method, the holozoic, and the parasitic. Among the latter is the organism[1] (Fig. 170 *C*, *D*) which, transmitted by a biting fly, causes the sleeping sickness of South Africa. Reproduction by syngamy takes place in some species, particularly in a few colonial flagellates. In some of these, like *Pleodorina*, the colony is differentiated into soma cells and germ cells. The latter become megagametes and microgametes, and zygotes are

[1] *Trypanosoma gambiense.*

formed from which new colonies originate. In other flagellates, where reproduction is entirely asexual, there is apparently no such thing as death from old age. The organism divides to give rise to two new organisms, and this process continues indefinitely unless individual cells are destroyed by physical or biological accidents. Many flagellates are able to weather unfavorable conditions by cyst formation, as do some algae and most bacteria.

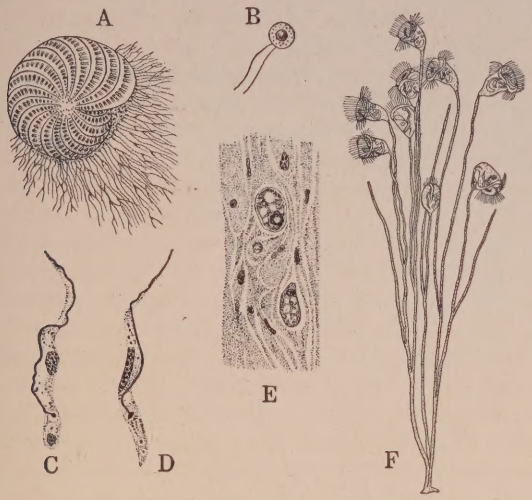

FIG. 170. — Protozoa. A, *Polystomella crispa*, a foraminiferan (after Lister); B, same, a gamete (after Schaudinn); C, *Trypansoma gambiense*, a flagellate, cause of sleeping sickness, as found in the gut of the tsetse fly; D, same as seen in the blood of infected mammals (both after Kleine and Taute); E, *Endamoeba dysenteriae*, in tissue of human intestine (after Doflein); F, *Carchesium polypinum*, colonial ciliate. (After Doflein.)

Sarcodina. — The Sarcodina include all the protozoa which move by pseudopodia, like *Amoeba*. They are mostly holozoic, although some, such as the species[2] (Fig. 170 *E*) which causes amoebic dysentery, are parasitic. Several groups of the Sarcodina secrete exoskeletons. The **Foraminifera** (Fig. 170 *A*) build microscopic shells of calcium carbonate, and these, sinking in the sea, for many of the Foraminifera are found in the zoöplankton, build up great beds of chalk. Another group of the zoöplankton, the **Radiolaria,** secrete beautiful tests of silica, and these

[2] *Endamoeba dysenteriae.*

form deposits of radiolarian ooze on the sea bottom. Many of the Sarcodina form flagellated swarm spores at some time in the life cycle. The Myxomycetes discussed in the last chapter are often considered protozoa and placed in this group under the heading Mycetozoa. Both sexual and asexual methods of reproduction are common among the Sarcodina.

Infusoria. — The Infusoria, as the ciliated protozoa are called, are divided into the **Ciliata,** which are ciliated throughout the life cycle, and the **Suctoria,** in which the cilia are present only in the early stages of the cell and are later replaced by tentacles. Most of the Ciliata, e.g., *Paramecium,* are holozoic, although some saprozoic and a few parasitic forms are known. The method of locomotion by the coördinating beating of many tiny cilia would seem to demand some sort of coördinating mechanism, such as is indicated through the existence of numerous fibers converging in a common center near the nucleus. In most ciliates there are two nuclei (Fig. 67), a meganucleus which appears to be a center of enzyme formation and a micronucleus. The latter always divides by mitosis, the former amitotically. Conjugation, including a reciprocal interchange of micronuclear material comparable to fertilization, and endomixis which may be compared with parthenogenesis, have already been mentioned. At times when these take place there is a mixture of nuclear and cytoplasmic materials which may have a rejuvenating effect. Otherwise reproduction is entirely by cell division.

The Suctoria reproduce by spore formation. The spore develops into a ciliated embryo which later becomes attached and develops the tentacles employed in the capture of food. It is interesting to note that the ciliated embryos often parasitize other protozoa.

Sporozoa. — The Sporozoa are a heterogeneous group placed together because they lack locomotor organs during the greater part of the life cycle, and are always of parasitic habit, together with the fact that spore formation is always characteristic of the life cycle. The group probably includes both Flagellata and Sarcodina which have been so modified by their parasitic habit as to have lost completely their distinguishing locomotor organs. They are divided into two groups: the **Telosporidia,** in which the individual organism is completely used up in spore formation, and the **Neosporidia,** which form spores at intervals during the life of the individual. The malaria organism, *Plasmodium* (Fig. 122), the causative agent of malarial fever, is a good example of a

type with an alternation of hosts accompanied by an alternation of generations. The chill characteristic of malaria — this type of malaria — occurs every forty-eight hours, as a new swarm of asexually produced *Plasmodia* is released. In the female mosquito, the organisms give rise to megagametes and microgametes, and syngamy followed by spore formation takes place. The spores enter the blood with saliva secreted by the mosquito.

PORIFERA

The existence of colonial flagellates with a differentiation into soma and germ cells, e.g., *Pleodorina* (Fig. 70), may indicate the starting-point of metazoan evolution. Two groups of relatively low organization are known, the Porifera or sponges and the Coelenterata. The phylum Porifera includes a number of interesting marine and a few fresh-water organisms characterized by the absence of a mouth and the presence instead of a number of tiny pores. Through these the water is sucked by the beating of flagella found on the collared cells of the inner (**gastral**) epithelium. Cells of this type are found among the flagellata (**Choanoflagellata**), which may indicate the evolutionary origin of the sponges. The tiny organisms and organic débris which are sifted through the pores are entangled in these collars while the water sweeps out through a single large opening (the **osculum**). There is an outer non-flagellated layer (the **dermal** epithelium), and between the two a layer of secreted mesogloea in which wander amoeboid cells. All sponges are sessile and apparently lack a neuro-motor system. Both simple sponges and colonial groups are known. Three classes are distinguished

FIG. 171. — *Spongilla fluviatilis*, a fresh-water sponge. (After Johnson.)

according to the material of which the skeleton is formed. In the **Calcarea** (Fig. 171), spicules of calcium carbonate are formed; the **Hexactinellida** have siliceous spicules; whereas the **Demospongia,** of which our common bath sponge[3] is an example, secrete fibers of **spongin,** a substance whose chemical composition is similar to silk. Reproduction may be asexual, by bud formation, or sexual. Sponges are hermaphroditic.

COELENTERATA

The Coelenterata are distinguished by the fact that the organisms have a single opening into a digestive cavity, an inner layer of endoderm, an outer layer of ectoderm, and between the two a mesogloea with wandering cells. *Hydra*, already described, is essentially a two-layered bag with an opening surrounded by tentacles. These contain curious cells armed with coiled poisoned threads which when forcibly ejected serve to paralyze the prey. The food is pushed down into the mouth and digested, after which the indigestible material is voided through the same opening. The neuro-motor mechanism has been described in Chapter V. Reproduction is asexual, by bud formation, or sexual.

Hydrozoa. — Three classes of coelenterates are distinguished. The Hydrozoa, of which *Hydra* is an example, discharge their sexual products to the exterior and have no gullet or mesenteries. Both hydroid and medusoid types are found, the latter being essentially a hydroid turned upside down and the mouth pushed back into the coelenteron. The hydrozoan medusae have a ring or velum partially closing the opening of the umbrella-like cavity. By the contraction of the body wall, water is forced out through the opening of the velum, so propelling the medusa through the water. Both solitary and colonial hydroid and medusoid species exist and in many, like *Obelia*, an alternation of generations between hydroid and medusoid generations takes place. In these colonies both hydroid and medusoid types are variously modified for purposes of locomotion, ingestion of food, protection, and reproduction. The medusoid generation usually reproduces sexually, and the hydroid generation usually reproduces asexually, but this is not always the case.

Scyphozoa. — The Scyphozoa spend most of the life cycle in the medusoid stage (Fig. 172). The fertilized egg develops into

[3] *Euspongia officinalis.*

a *Hydra*-like form which reproduces by budding but finally is constricted into a series of disks, each of which develops into a medusa without a velum. There is a gullet between mouth and coelenteron supported by folds called mesenteries. Most of our large jellyfish belong to this group.

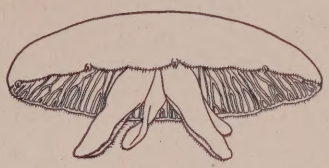

FIG. 172. — *Aurelia aurita*, one of the scyphozoan jellyfish. (After Johnson and Snook.)

Actinozoa. — The Actinozoa are exclusively hydroids or polyps. The mouth opens into a gullet and this into the coelenteron which is divided radially by a number of partitions called mesenteries. The group includes both simple and colonial forms, many of which secrete about the individual polyps a skeleton of calcium carbonate. These are the so-called coral-forming polyps (Fig. 173), through whose

FIG. 173. — *Euplexaura marki*, one of the coral-forming actinozoans. The individual polyps project from the coral branch. (After Johnson and Snook.)

activities coral reefs and islands come into being, although it must be remembered that a large part of this work is done also by the red algae.

PLATYHELMINTHES

With the **Platyhelminthes** or flatworms, we enter the world of three-layered (triploblastic) animals. These are marine, freshwater or parasitic organisms, with bilateral symmetry and three germ layers from which arise digestive, excretory, reproductive, muscular, and nervous systems. There are three classes.

Turbellaria. — The Turbellaria are free-living flatworms, mostly aquatic, e.g., *Planaria*. This organism has a mouth with

a protrusible pharynx (or proboscis) and a highly branched intestine, but no anus. The branching of the intestine eliminates the necessity of a circulatory system. Wastes are disposed of

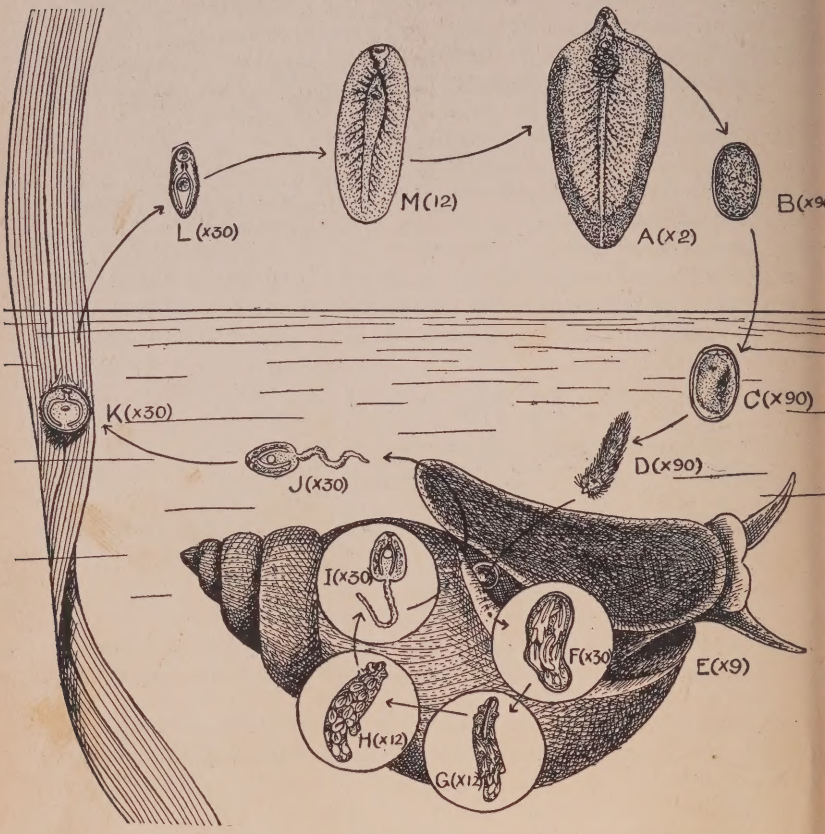

FIG. 174. — Life history of *Fasciola hepatica*, the liver-fluke. A, adult in sheep liver; B, egg; C, unhatched embryo; D, miracidium; E, snail; F, sporocyst; G, redia; H, second generation redia; I, cercaria; J, swimming cercaria; K, encysted cercaria on grass; L, cercaria in gut of sheep; young fluke in liver. (From Chandler, "Introduction to Human Parasitology," John Wiley and Sons, Inc.)

through two longitudinal coiled nephridial tubes opening to the exterior by pores on the dorsal surface. These tubes are formed by the union of many finer tubes, each originating from a large

hollow "flame" cell with a brush of cilia in the cavity. The nervous system consists of two longitudinal nerve trunks united by cross fibers and fused at the anterior end into a cerebral ganglion, from which fibers pass to the surface. A pair of pigment spots represent eyes. Locomotion is by means of cilia developed by the ectodermal cells and by the contraction of the muscles developed in the mesoderm. An elaborate hermaphroditic reproductive system opens to the exterior by a genital pore. Fertilization is internal.

Trematoda. — The Trematoda are internal or external parasites in which the ectoderm is not ciliated and a sucking disk (or disks) is present. The liver-fluke, *Fasciola* (Fig. 174), is a parasite in the bile ducts of domestic animals such as the sheep, pig, cow, etc., and sometimes of man. It has two suckers, in the more anterior of which the mouth is located. There is no anus and the intestine is branched as in *Planaria*. The excretory system has a single duct and pore. An elaborate hermaphroditic reproductive system adapted to internal fertilization is present, opening to the exterior by a genital pore. The muscles and nervous system resemble those of *Planaria*, but no eyespots are found. The internal organs are packed in a loose connective tissue, the parenchyma. The life history is a complicated one. The zygote, which passes out of the host's body with the feces, develops in water into a ciliated larva (**miracidium**). This bores into the body of the intermediate host, a fresh-water snail, and encysts after a couple of weeks to form a **sporocyst.** The sporocyst produces parthenogenetic eggs which develop into **rediae.** These may give rise to one or more generations of rediae asexually but eventually produce, also asexually, tailed larvae known as **cercariae.** The cercariae are voided by the snail, swim about for a time, and finally encyst on grass. If eaten by the sheep, the cercaria emerges from its cyst and makes its way through the intestine to the bile duct, where it assumes the appearance of the adult fluke.

Cestoda. — The Cestoda include the endoparasitic tapeworms such as *Taenia* (Fig. 175). The body is either simple or compound. The majority are compound, with a terminal attaching head (**scolex**) often armed with hooks and suckers, and a row of **proglottids,** or reproductive segments, budded off from the scolex. No digestive system is present, as the food is absorbed through the body wall (saprozoic nutrition). Each proglottis has a pair of nerve cords, a pair of nephridial ducts and an elaborate

hermaphroditic reproductive system packed in parenchyma. It is believed that self-fertilization is the rule. The muscles are poorly developed. The fertilized egg while still within the egg membrane develops into a six-hooked embryo before leaving the proglottis. If eaten by a pig, the intermediate host, the embryos hatch and bore their way through the intestine into the skeletal muscles, where they encyst and become transformed into bladder worms (**cysticerci**), with an inverted scolex growing into the cavity of the cyst. If the pork is eaten by man, without adequate cooking, the scolex is everted, attaches to the wall of the digestive tube, loses the cyst and begins to bud off proglottides.

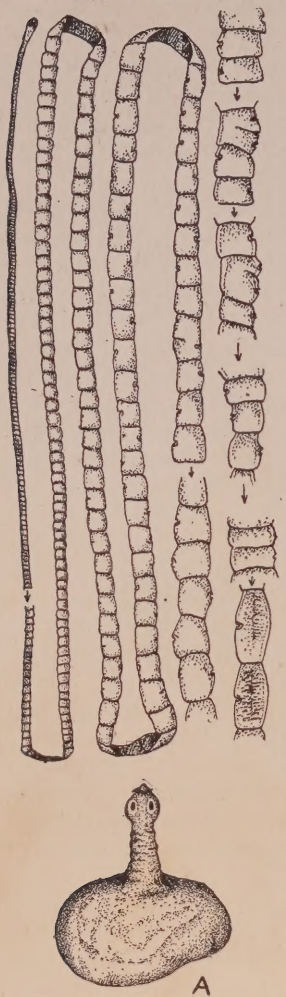

FIG. 175. — Tapeworm, *Taenia saginata*, and A, cysticerus of *T. solium*. (After Stiles, from Chandler.)

NEMATHELMINTHES

The phylum **Nemathelminthes** or roundworms includes triploblastic, bilaterally symmetrical animals with a digestive tube opening at both ends and enclosed in a body cavity. Both free-living and parasitic nematodes are known. They differ from the flatworms also in that the sexes are separate. Specialists believe that the body cavity may represent an open vascular system. The free-living nemas are found in the soil and water. One curious species is the vinegar eel, which lives in vinegar. The parasitic forms are endoparasites in the cavities of the body and sometimes in the tissues. Several dangerous human parasites are included in this phylum, among them *Trichinella*, the cause of trichinosis, and *Necator*, the hookworm of the Southern states and the tropics.

Trichinella (Fig. 176) is a parasite of man, pig, and rat. It is contracted by humans through eating infected pork which has not been sufficiently cooked. The larvae mature and reproduce rapidly in the intestine, and the young bore their way to all the

Fig. 176. — A parasitic nematode, *Trichinella spiralis*, burrowing in human muscle, before encystment. ×75. (From Chandler.)

muscles of the body, where they encyst. Rats become infected from human offal, and pigs in the same manner or by eating infected rats.

Necator larvae develop in moist soil and make their way into the human body by boring through the skin of the bare foot. Entering the blood vessels, they are carried in the blood stream to all parts of the body, but particularly to the intestine, where the adults attach themselves and obtain their food from the blood of the host. The lung also is infested, so that sufferers are anaemic and subject to tuberculosis. The inertia of the so-called poor whites is largely due to the anaemia brought on by the presence of these parasitic nematodes. Preventive measures consist in the proper disposal of human feces and the use of protective foot-wear. Vermifuges, which cause the worm to detach itself from the intestinal wall, followed by cathartics will free the digestive tract from these parasites.

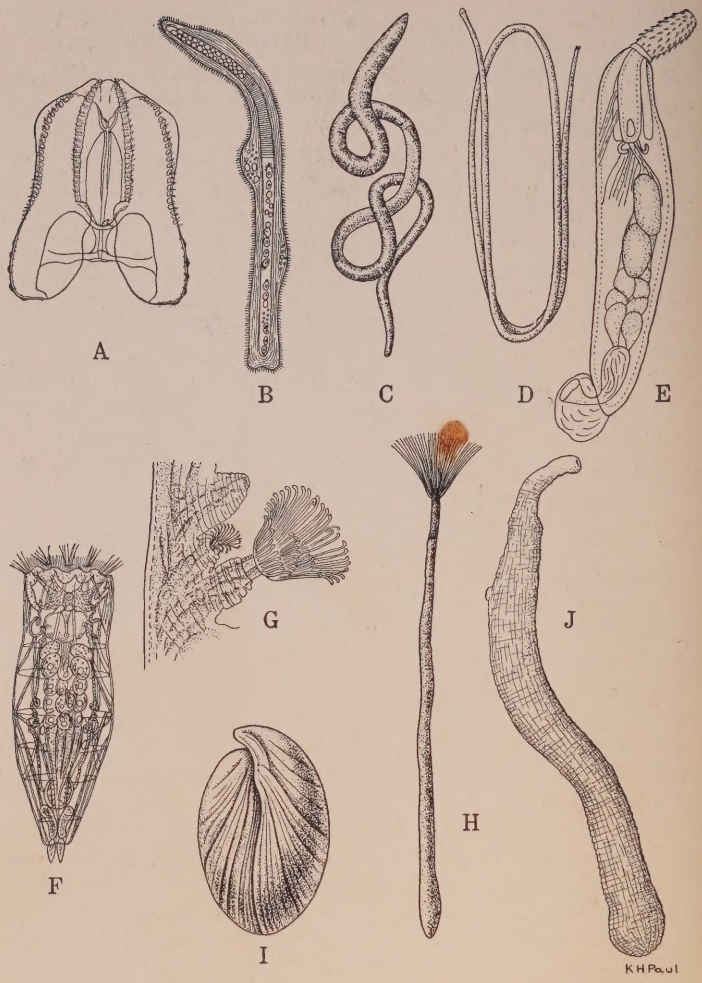

FIG. 177. — Invertebrates of uncertain position. A, ctenophore, *Bolenopsis microptera* (after Johnson and Snook); B, mesozoan, *Dicyema paradoxicus* (after Kölliker); C, *Micrura verrelli*, a nemertean (after Coe); *Gordius*, a threadworm; E, *Acanthocephalus ranae* (after Van Cleave); F, *Hydatina senta*, a rotifer (after Weber); G, *Plumatella punctata*, part of a bryozoan colony (after Kraepelin); H, *Phoronis australis* (after Parker and Haswell); I, a brachiopod, *Magelliana flavescens* (after Davidson); J, a gephyrean worm, *Sipunculus nudus* (after Johnson and Snook).

INVERTEBRATES OF UNCERTAIN POSITION

A number of small groups of uncertain position may be briefly mentioned at this point before proceding further. The **Ctenophora** (Fig. 177 *A*) or seacombs are a type of marine jellyfish a little more highly organized than the medusae and sometimes placed in a separate phylum. The **Mesozoa** (Fig. 177 *B*) include a number of parasites of low organization. Nearly all have now been assigned to other groups, especially to the Platyhelminthes. The **Acanthocephala** (Fig. 177 *E*) are parasitic worms possibly allied to the Nemathelminthes. The **Chaetognatha** are marine arrow-worms which are thought to have nematode affinities. The **Nemertini** (Fig. 177 *C*), not to be confused with the nematodes, are ciliated roundworms which may belong near the flatworms. The common horse-hair worm (*Gordius*) (Fig. 177 *D*), belonging to the **Nematomorpha,** is found in watering-troughs and believed by the ignorant to arise from a horse hair taking on life. In reality the larva spends its life in the body cavity of grasshoppers and aquatic insect larvae. The **Rotifera** (Fig. 177 *F*) or wheel-animalcules are microscopic triploblastic aquatic forms without a true coelom but with a digestive tube. There is an alternation of generations between parthenogenetic and syngametic forms. Some of the simpler rotifers resemble the aquatic larvae of the annelids and molluscs. The **Bryozoa,** or moss-animalcules (Fig. 177 *G*), mostly marine, are colonial forms superficially resembling hydroid colonies but differing in their higher organization. The **Phoronidea** (Fig. 177 *H*) include a single marine genus of tube-dwelling worms with some characters like those of the Bryozoa. The **Brachiopoda** (Fig. 177 *I*), formerly placed with the Mollusca because of the bivalve shell, are now placed near the Bryozoa. They are coelomate animals of great antiquity. Brachiopod shells from Silurian rocks are often identical with modern species. The **Gephyrea** (Fig. 177 *J*) are unsegmented coelomate worms sometimes placed near the Annelida.

The Coelomata. — Some of the problematic groups mentioned in the preceding paragraph possess body cavities lying between the wall of the digestive tube and the body wall. Such a cavity adds greatly to the efficiency of the animal. The separation of the gut from the body wall permits the development of two different sets of muscles appertaining to the gut and the body wall, respectively, and allows the development of coils and

diverticula by which the absorptive surface of the gut wall is increased. Within the cavity itself the viscera are suspended by mesenteries and often bathed in a coelomic fluid. Different types of coeloms are distinguished by the morphologist, according to the embryological development and functions subserved. All of the remaining phyla are coelomate.

ECHINODERMATA

The Echinodermata are exclusively marine animals with a peculiar type of radial symmetry based on the number five. The skin is covered with a skeleton of calcareous plates, often with

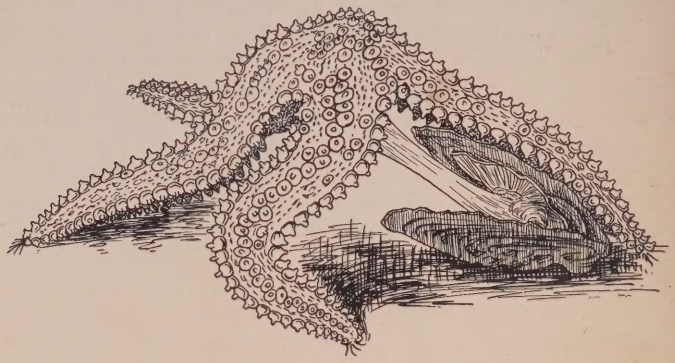

FIG. 178. — Starfish (*Asterias glacialis*) devouring oyster. (After Hesse-Doflein.)

spines. The phylum includes five classes: the Asteroidea or starfishes (Fig. 178), Ophiuroidea or brittle-stars, Echinoidea (Fig. 179 *B*) or sea-urchins, Holothuroidea (Fig. 179 *C*) or sea-cucumbers, and Crinoidea (Fig. 179 *A*) or sea-lilies. The last group are the survivors of a subphylum which had far more species in the Palaeozoic Age.

In the common starfish, *Asterias*, there are five arms in the common center of which, on the lower side, is the mouth, while the anus is on the upper surface. Between the bases of two arms is a plate containing the opening of the water-vascular system which is concerned with locomotion. Water driven into the system by cilia is forced into tiny sacs at the inner end of the tube feet found on the ventral surface. When this sac is contracted by its circular muscle, the lower end of each tube

foot is flattened against the object on which it is resting, and a partial vacuum is created. The contraction of longitudinal muscles in the tube foot now draws the arm slowly along in the direction in which the tube foot had been stretched out. In eating molluscs, which form a large part of the diet, the starfish seizes the prey with its tube feet, wraps the arms about it, humps itself up, and by contraction of the tube feet exerts a slow continuous pull to which the muscles of the mollusc finally yield.

FIG. 179. — Echinoderms. A, *Metacrinus rotundus*, a sea-lily (after Hesse-Doflein); B, *Arbacia punculata*, a sea-urchin (after Coe); C, *Thyone briareus*, a sea-cucumber (after Coe).

In the meantime the pressure exerted by the muscles of the arms transmitted through the coelomic fluid force the stomach inside out. It is pushed between the gaping valves, and wrapped around the body of the mollusc, which is practically digested within its own shell. The fluids of the coelom around the digestive tract which are kept in motion by cilia, transport the absorbed food to various parts of the body. Amoeboid cells in the fluid are believed to act as scavengers of waste materials. The coelom extends into tiny projections on the aboral (upper) surface which act as respiratory organs. A nerve ring around the mouth re-

ceives a nerve cord in each arm connected with the tube feet, which act as tactile sensory organs, and with pigment spots at the tip of each arm which are light-percipient. The aboral muscles of the arms are innervated by an apical system with a trunk in each arm. The sexes are separate, and the eggs and sperm are discharged through pores on the aboral surface between the bases of the arms. Fertilization is external, and a bilaterally symmetrical ciliated larva (**bipinnaria**) is formed. This swimming larva is transformed into the starfish. As the eggs and sperm are formed in large numbers and are easily handled and preserved, they have long served as material for experimental embryology.

ANNELIDA

With the phylum **Annelida** we come to one which is more familiar. The segmented worms are found on land, in fresh water, and the sea. With the exception of a few ectoparasites

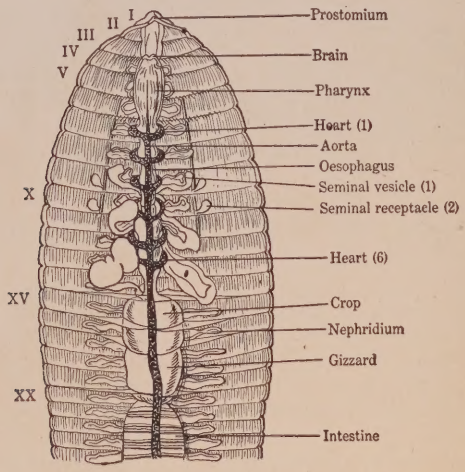

FIG. 180. — Dissection of the earthworm, *Lumbricus terrestris*, from dorsal side. (After Hatschek and Cori.)

all are independent. The earthworm, *Lumbricus terrestris* (Fig. 180), already mentioned, illustrates the phylum. The body is essentially a tube within a tube. The outer tube or body wall is divided into segments by grooves on the surface. There

are over a hundred segments in adult worms, of which six (XXXII to XXXVII), are swollen to form a **clitellum** used in reproduction. Each segment except those at the ends has four pairs of bristles, each with a pair of muscles. Two layers of muscles underlie the skin. The inner tube is the digestive tube, with a mouth at one

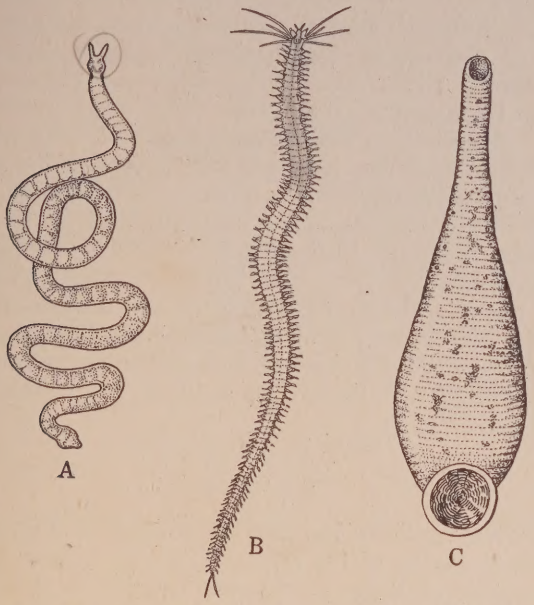

FIG. 181. — Annelid worms. A, *Polygordius*, an archiannelid (after Whitman); B, *Nereis*, a polychaete worm (after Newman); C, a leech.

end, vent at the other, and a series of specialized regions between. The food is sucked into the mouth and propelled through the digestive tube, while the digested material is absorbed and distributed by a vascular system with a number of beating hearts. Wastes are disposed of through a pair of nephridial tubes in each segment, except the first three and the last, for the coelom between body wall and gut is divided by partitions corresponding to the grooves on the surface already mentioned. The tubes open into the coelom and discharge their contents to the exterior by pores. Each coelomic cavity also opens to the exterior by a pair of tiny dorsal openings. The nervous system is made up of a cephalic ganglion (segment III) receiving neurones from a

short proboscis over the mouth. This is connected by a band running around the gut to a pair of ventral ganglia (segment IV) which send back a nerve cord. The cord enlarges to form a ganglion in each somite which sends out three pairs of nerves. Sensory hairs are the principal sense organs. The earthworm is hermaphroditic but reproduces by cross-fertilization. The worms adhere to each other in such a way as to bring the ventral surfaces of the clitella together and exchange spermatozoa. A slimy secretion from the clitellum encloses a cocoon in which eggs and sperm are discharged, after which the worm withdraws its head. Fertilization and the early stages of embryology take place within the cocoon, and the worms hatch in a few weeks.

There are three classes of worms: the **Archiannelida** (Fig. 181 *A*), without setae, including only a few marine forms; the **Chaetopoda** (Fig. 181 *B*), including terrestrial fresh-water and marine worms, many of which are highly organized and strikingly colored; and the **Hirudinea** (Fig. 181 *C*), or leeches, having no setae, only thirty-three segments, and a sucker at each extremity. All the forms have a true coelom, are metameric, and most of the marine forms pass through a trochophore larva stage in their embryology.

MOLLUSCA

The phylum Mollusca includes the shellfish, and is one of the three largest groups of the animal kingdom. There are about 60,000 species of these unsegmented coelomate animals, the majority of which are protected by exoskeletons of calcium carbonate. Clams, snails, and octopi all resemble each other in the possession of a foot used by the clam for burrowing, the snail for crawling, and the octopus for seizing its prey. All are surrounded by a membrane, the **mantle,** enclosing a mantle cavity into which the digestive tube opens.

The fresh-water clam, *Anadonta* (Fig. 182), will serve as an example. The two valves are united at the dorsal edges by a ligament which serves as a hinge. They are secreted by the two folds of the mantle which enclose the remainder of the body. The shells are held together by the contraction of two large transverse muscles. When these relax, the compressible elastic ligament forces the valves open. The folds of the mantle protrude at the posterior end to form a ventral incurrent siphon and a dorsal excurrent siphon. These direct the circulation of water

driven by the beating of numerous cilia on the gill flaps, which hang down inside the mantle cavity. Food particles are directed into the mouth at the anterior end by cilia on triangular flaps surrounding it, and the undigested remains are defecated through the vent at the posterior end of the mantle cavity. There is a circulatory system, consisting of a heart, anterior and posterior vessels, and numerous spaces or sinuses. Respiration takes place in the gills and the mantle. Two kidneys ex-

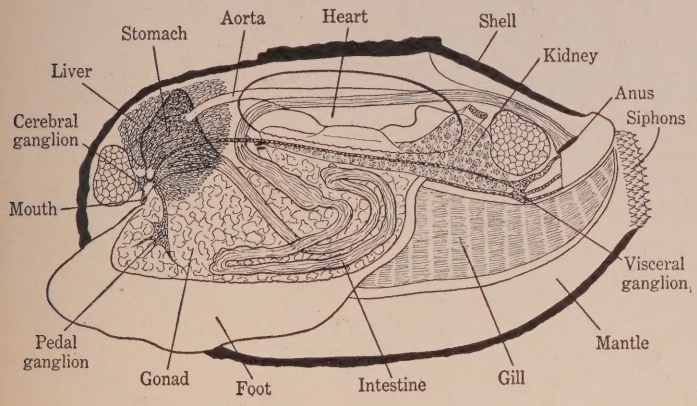

FIG. 182. — Dissection of a fresh-water clam, *Anadonta mutabilis*, from left side. (After Hatschek and Cori.)

tract waste from the pericardial cavity surrounding the heart directly, and from the blood vessels by a glandular body, and discharge it into the mantle cavity near the excurrent siphon. The nervous system consists of ganglia near the mouth, the kidneys, and in the foot, connected by nerve cords. In the foot is an equilibratory organ; near each visceral ganglion is found a sensory patch which is thought to test the water entering the ventral siphon. The mantle is provided with many sensory cells, mechanoreceptors, and photoreceptors. Reproduction is generally dioecious, although some hermaphroditic species are known. The eggs are discharged from the gonad and are caught in the gills. The sperm entering the incurrent siphon fertilize the eggs which develop into a peculiar larva known as the **glochidium.** This is a bivalve form with a long sensory thread which stimulates the valves to close on touching the body of a fish. Thus attached, the glochidium is surrounded by a skin growth

known to fishermen as a blackhead. Here the larva develops parasitically and finally becomes transformed into a miniature adult, when it is released to take up an independent existence.

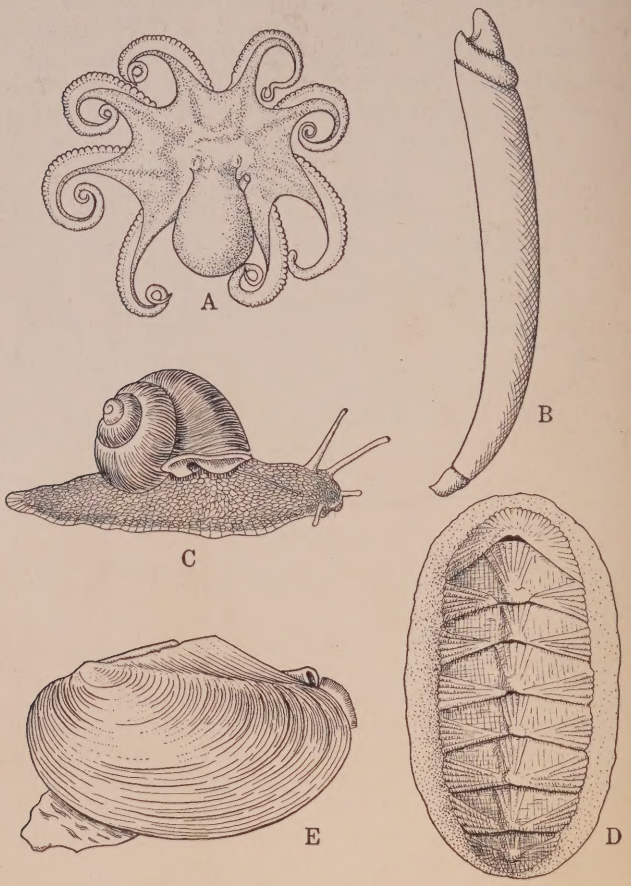

FIG. 183. — Molluscs. A, *Octopus* (after Cowdry); B, *Dentalium*, C, *Helix* (after Hatschek and Cori); D, *Anadonta* (after Howes); E, *Ischnochiton cooperi.* (After Johnson and Snook.)

There are five classes of Mollusca. The **Amphineura** (Fig. 183 *D*) include a number of marine forms without shells or with a series of plates on the dorsal surface. The **Gastropoda** (Fig.

183 *C*) include the air-breathing snails and slugs, some fresh-water and very many marine snails, most of which have a coiled shell, well-developed head, and crawling foot. The **Scaphopoda** (Fig. 183 *B*) include a few sand-dwelling marine forms commonly known as tooth shells. The **Pelecypoda** include bivalves like *Anadonta* (Fig. 183 *E*), the oyster, etc. The **Cephalopoda** is a group which today includes the octopus, squid, and nautilus, but in the Palaeozoic Age included many more swimming shellfish. Some of these, like the octopus (Fig. 183 *A*), have lost the shell completely. The foot is divided into arms provided with sucking disks, and the mantle has two openings, a collar around the mouth and a movable siphon. Water taken in through the collar is expelled through the siphon to propel the animal forward or backward according to the direction in which the siphon is pointed. Well-developed eyes with iris, lens, and retina are formed, and a number of ganglia are present, mostly in the head. Both squid and octopi grow to great size, the largest recorded octopus having an arm spread of over thirty feet. If were it not for the existence of marine vertebrates, these cephalopods would be the dominant animals of the sea.

ARTHROPODA

The Arthropoda are bilaterally symmetrical, coelomate, metameric animals with a chitinous exoskeleton and jointed appendages. They include the crustaceans, centipedes, insects, spiders, etc. Because of the inclusion of the insects with over half a million species, this phylum is the largest in the animal kingdom. Five classes are distinguished: the **Crustacea, Onychophora, Myriapoda, Insecta, and Arachnida.**

Crustacea. — The Crustacea are mostly marine forms, although there are many fresh-water and some few terrestrial types. They range from the microscopic Entomostraca found in marine and fresh-water plankton to gigantic lobsters and huge spider crabs, with a leg spread of over twenty feet. Some forms are sessile like the barnacles; others are ectoparasites whose larvae alone reveal their arthropod affinities, like *Sacculina* already described. In the earliest fossiliferous rocks are found extinct Crustacea belonging to the group **Trilobita.** (Fig. 137.)

The fresh-water crayfish, *Astacus fluviatalis* (Figs. 184, 185 *A*), will serve as an example of the higher Crustacea. The segments in the anterior part of the body are obscured by the develop-

ment of a **carapace.** This covers the cephalothorax which includes the head and thorax (segments I–XIII), with a transverse groove marking the line of junction. The abdomen includes six segments (XIV–XX) each with a **tergum** covering the dorsal surface, also lateral and ventral plates. The abdomen terminates in

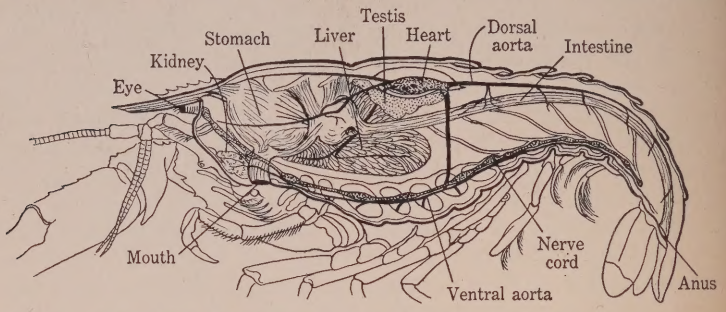

FIG. 184. — Dissection of the crayfish, *Astacus fluviatalis*, from the left side. (After Hatschek and Cori.)

the **telson** (segment XXI). Each segment bears a pair of jointed appendages, specialized for purposes of sense perception, seizing and crushing food, walking, cleaning the abdomen, transferring sperm (in male), creating currents of water, swimming, etc. The true coelom is small, and the cavity around the viscera is a great blood sinus. The blood is sucked from this by the beating heart and propelled to various parts of the body by seven arteries. Under the carapace at the base of certain appendages are the gills in which the blood is oxygenated from a water current which is kept moving forward by the action of the swimmarets. Respiration is accomplished by a pair of kidneys much like those of the clam. The nervous system resembles that of the earthworm, but more specialized sense organs are present, i.e., the eyes on moveable stalks, the equilibrium organs in the bases of the first appendage, the tactile antennae, etc. The sexes are usually separate and the male transfers spermatozoa to the female in the fall. These are stored until the next spring when the eggs are fertilized and discharged to adhere on the swimmarets. After hatching, the young go through a series of molts characteristic of all growing Crustacea. The great disadvantage of the exoskeleton lies in the limits it imposes on growth and the consequent necessity of shedding the protective armor and growing a new and larger suit. In many of the higher Crustacea, the form assumed at each

molt differs and may even resemble the adult stages of less highly specialized types. Thus the shrimp *Penaeus* passes through four such stages known as the **nauplius, protozoaea, zoaea,** and **mysis.** This, it will be remembered, was the starting-point of the recapitulation theory (page 231).

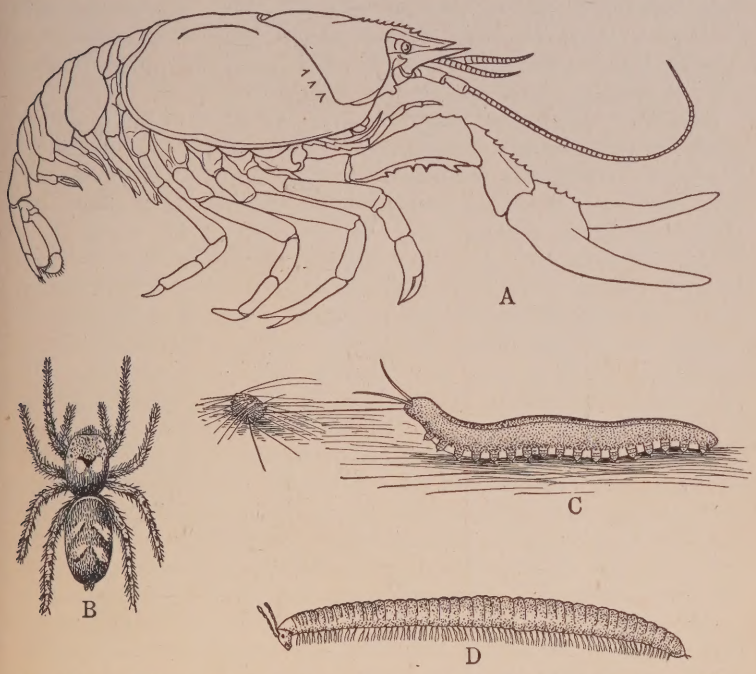

FIG. 185. — Arthropoda. A, *Astacus fluviatalis*, the crayfish, a crustacean (after Hatschek and Cori); B, *Attus*, the jumping spider, an arachnid (after Davenport); C, *Peripatus*, an arthropod with many annelid characters (after Sedgewick); D, a millipede (after Metcalf and Flint).

Onychophora. — The Onychophora include a single genus *Peripatus* (Fig. 185 *C*), famous among zoölogists because in many respects, e.g., tracheal respiration, it is intermediate between the Annelida and the Arthropoda.

Myriapoda. — The Myriapoda include the millipedes and centipedes, all terrestrial forms with very many jointed legs (Fig. 185 *D*). They also breathe by tracheal tubes, like the insects.

Arachnida. — The Arachnida include the spiders (Fig. 185 *B*), scorpions, ticks, and king-crabs, mostly terrestrial and breathing by tracheal tubes or book lungs, sacs with leaf-like shelves in which the air is brought into close proximity to the blood. They have four pairs of legs. Practically all are terrestrial, but the king-crab [4] is a sole survivor of a marine race. Its larva passes through a stage curiously reminiscent of the extinct trilobites. Among the Arachnida several parasites are known, the harvest mite or chigger, the ticks, the itch mite, etc.

Insecta. — With the insects we have come to a group whose members are largely terrestrial. Although a few protozoa, flatworms, nematodes, annelids, and molluscs live in damp soil, practically all the phyla mentioned in the preceding pages are aquatic groups. Among the Crustacea there are some land crabs, sow-bugs, etc.; the other groups are mainly land dwellers; but the insects show the most perfect adaptation to terrestrial life. This is reflected in the enormous number of species recorded, over half a million, which is more than a half of all known organisms, both plants and animals. This group, like the Spermatophytes among plants, is a relatively late-comer, for the first fossil insects occur in the Pennsylvanian period.

The insects are divided into orders on the basis of such characters as the number and kind of wings, the kind of mouth-parts (biting, sucking, etc.), and the type of development, i.e., the presence or absence of metamorphosis (page 287). But before discussing the classification of the insects, it is necessary to consider the anatomy of some common species as a foundation.

We use a roach (*Periplaneta*) (Fig. 186) as an example of insect anatomy. The body is divided into three main parts, head, thorax, and abdomen. The head has a single pair of antennae, a compound eye on each side, three simple eyes in front, and four pairs of mouth-parts. The thorax is made up of three segments each bearing a pair of legs. The second and third segments bear a pair of wings. The abdomen contains eleven segments, seven of which have spiracles or breathing pores for the tracheal system, while the thorax has two such pairs. The posterior segment is modified for reproductive purposes, the female bearing an egg-laying tube, while the male is provided with copulatory organs. The digestive tube is subdivided into regions where the several steps of digestion are carried on, and the absorbed foodstuffs are distributed by the blood. The vascular sys-

[4] *Limulus polyphemus.*

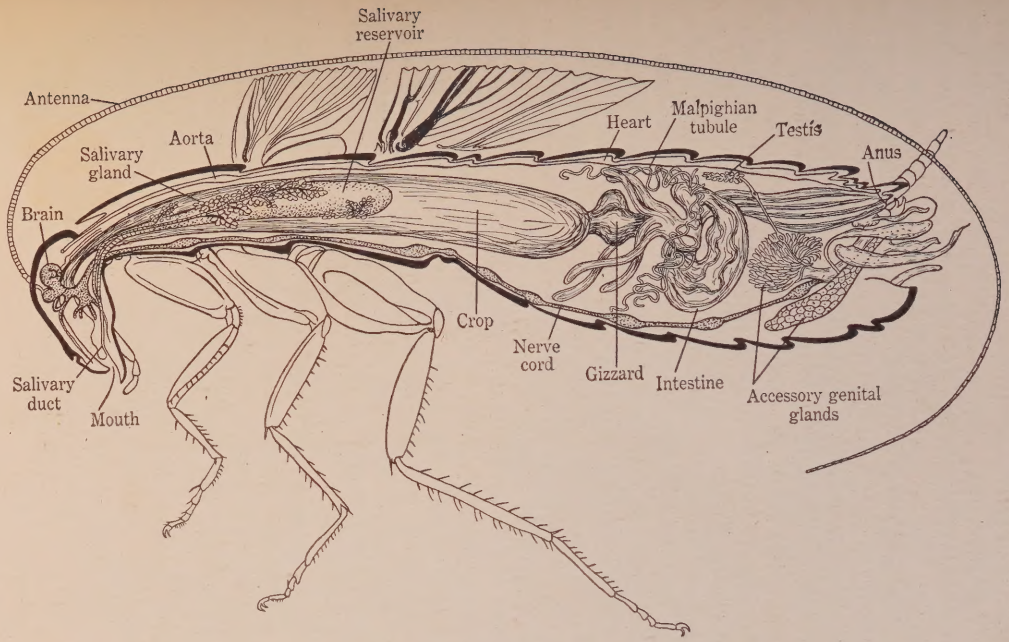

FIG. 186. — Dissection of *Periplaneta*, the cockroach, from the left side. (After Metcalf and Flint.)

tem is an open one, in which the heart forces the blood forward through a short aorta into the **haemocoele** and receives it again at its posterior end. The sluggish flow of the blood is correlated with the tracheal system of breathing which is characteristic of insects. The air entering the spiracle is transported through tubes (**tracheae**) which branch tree-like and penetrate every part of the body so that atmospheric oxygen is everywhere available. Excretion is carried on by Malpighian tubules (named after their discoverer, Malpighi, 1628–1694), thread-like extensions of the intestine which lie in the haemocoele and discharge the wastes extracted by them into the intestine, to be voided with the feces. The muscular system as in all the arthropoda is attached to the exoskeleton. An elaborate central nervous system is found, with a brain composed of two optic lobes and a median mass arising from the fusion of three pairs of ganglia. Commissures connect this brain with a ventral ganglion, and this in turn is connected with paired ganglia corresponding to the thoracic and abdominal segments. A sympathetic system of ganglia innervates the digestive system. The sense organs are the eyes, antennae which are both tactile and olfactory organs, tympanic or auditory organs on either side of the first abdominal segment, and tactile hairs scattered over the body. The sexes are separate, fertilization is internal, and the eggs laid in the fall in the topsoil hatch in the following spring. The young go through a series of molts but pass through no larval stages in which the form differs from that of the adult.

So large a group as the Insecta is divided into many subgroups, most authorities recognizing nineteen to twenty-five orders. Within the short space available here, however, we shall retain the older condensed classification which contains only nine orders.

Aptera. — The first, Aptera, includes the wingless insects, with biting mouth-parts and a direct development without larval stages. Among this group we find the fishmoth[5] (Fig. 187 *I*), which lives on starch found in bookbindings, wall paper and linens. It is a small group with only about 900 species.

Pseudoneuroptera. — The Pseudoneuroptera include the insects with two pairs of similar wings, biting mouth-parts and incomplete metamorphosis. The may-flies (Fig. 187 *D*) spend the greater part of the year (sometimes two or three) as aquatic larvae or nymphs (Fig. 187 *E*), whereas they spend but a few hours in

[5] *Lepisma saccharina.*

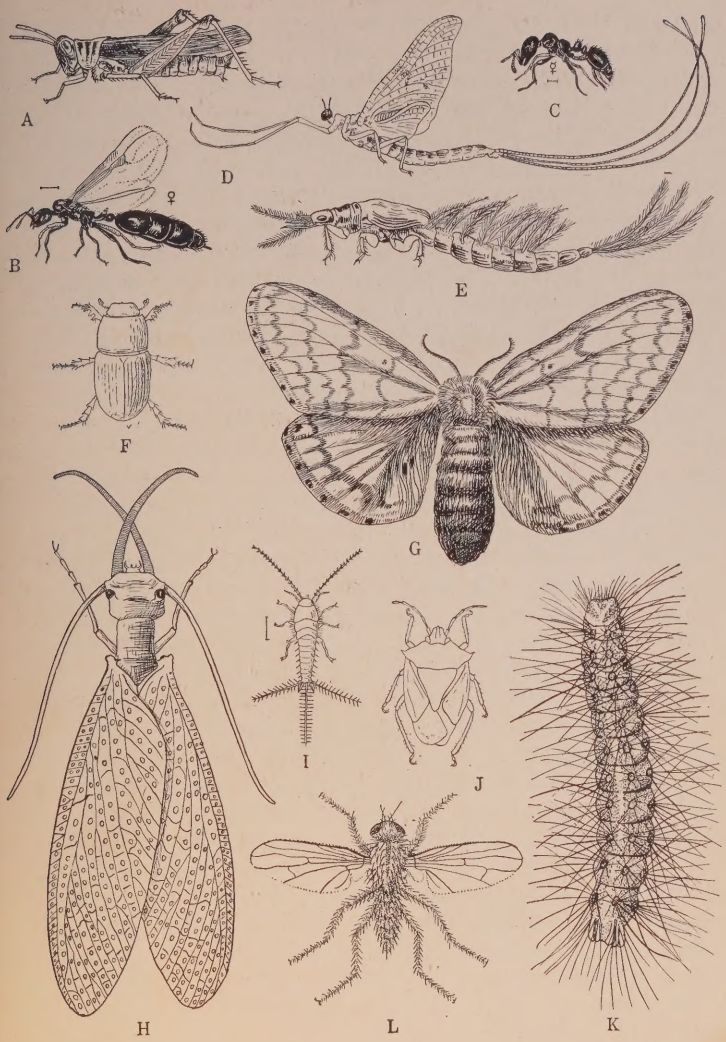

FIG. 187. — Insects. A, *Melanoplus femur-rubrum*, a grasshopper; B, *Monomorium minimum*, a winged female ant; C, worker of the same species; D, *Ephemera varia*, an adult may-fly; E, nymph or aquatic larva of the same species; F, *Aphodius granarius*, a beetle; G, *Porthetria dispar*, the gypsy-moth; H, *Corydalis cornuta*, a dobson-fly; I, *Lepisma saccharina*, a silverfish or wingless insect; J, *Thyanta perditor*, a bug; K, *Porthetria dispar*, caterpillar (see G); L, *Phorbia fusciceps*, a fly. (A, F, G, J–L after Forbes, B–E, H, I after Metcalf and Flint.)

the adult condition. Without mouth-parts, they can take no food, but mate, lay the eggs in water, and die. The stone-flies too spend a large period of their lives as aquatic larvae. The dragonflies and damsel-flies belong to this order. The young live in the water, while the adults prey on other insects, particularly the mosquito. The termites or " white ants " are assigned to this group. These are colonial insects, living in the dark and feeding on dead wood whose cellulose they digest through the aid of a commensal flagellate found only in the termite intestine. Four castes exist, a winged female (queen) winged male (king), wingless workers, and soldiers. The remaining groups include book-lice which devour old paper, bark-lice which feed on lichens, bird-lice, ectoparasites of birds and mammals, and thrips, usually parthenogenetic pests of cultivated plants.

Orthoptera. — The Orthoptera have two pairs of wings, of which the anterior pair are leathery while the posterior are membranous and fold under the first. The mouth-parts are biting, and metamorphosis is incomplete. In this group we find the earwigs, cockroaches, the curious praying-mantis whose prehensile fore-legs are folded in a most devout manner and the walking-sticks which mimic the twig on which they crawl. The grasshopper (Fig. 187 *A*) and cricket are examples of this order, as is the Rocky Mountain locust (not to be confused with the seventeen-year locust which belongs in the next order).

Hemiptera. — The Hemiptera (Fig. 187 *J*) or bugs are wingless or with four wings. The mouth-parts are adapted to sucking, and metamorphosis is incomplete. Three main subdivisions are distinguished, of which the first includes the parasitic lice, wingless blood-sucking forms such as the head-louse[6] of man. The second group includes those forms in which the two pairs of wings are similar. Here we find the plant-lice and phylloxerans, etc., destructive to many cultivated plants, the scale insects, and the cicadas. Here belongs the seventeen-year locust, which lives underground as a nymph for sixteen years, feeding on the sap in roots. Entomologists are acquainted with twenty races of this cicada and can predict when and where each will swarm. The harvest fly[7] is closely related. In the third group or true bugs the first pair of wings is thickened at the base. This group includes the water-boatmen, back-swimmers, water-striders, all of which are aquatic forms, and the bedbugs, the assassin bugs

[6] *Pediculus capitis.*

[7] *Cicada tibicen.*

which prey upon the last-mentioned pest, squash bugs, and other terrestrial forms.

Neuroptera. — The Neuroptera have four membranous wings with a complicated system of veins and biting mouth-parts. As distinguished from the Pseudoneuroptera they have a complete metamorphosis, that is to say, they pass through a larval and a **pupal** stage. In the latter the larva spins a cocoon within which it is slowly transformed into the adult. This group includes the dobson-fly (Fig. 187 *H*), the larva of which, sometimes called a helgramite, is used as fish bait. The larvae of other Neuroptera are known as ant lions. They dig pits in the sand at the bottom of which they lie concealed, ready to dart out and suck the blood of any ants that slip down. The scorpion-flies, so-called from the resemblance of the male abdomen to that of a scorpion, belong in this group, as do the caddice-flies, whose larvae build cases of leaves, sticks or sand grains for houses.

Lepidoptera. — The Lepidoptera include the butterflies and moths (Fig. 187 *G*). They have four membranous wings covered with scales, sucking mouth-parts, and a complete metamorphosis. Their larvae are well known as caterpillars (Fig. 187 *K*) and are often pests. The adults use the long coiled tube-like proboscis to suck nectar from the nectaries of flowers and are therefore considered one of the younger groups of Insecta for the flowering plants came late in evolution. The butterflies are distinguished from the moths by the knobs in which their antennae terminate. Also the butterflies are active during the day, whereas the moths are nocturnal. This group is well known to amateur biologists, and over 7000 species have been identified in the United States. Among the butterflies are many cases of what is called "protective mimicry" in which the insect resembles either some leaf or flower, as does the dead-leaf butterfly,[8] or some other insect which is not preyed upon by butterfly-eating animals. Many of the moths are well known because of the damage done by their larvae, such as the gypsy-moth,[9] the boll-worm,[10] and the codling-moth.[11] The larva of the clothes-moth[12] is known to every housewife. It is not the moth which does the damage, as generally believed, but the larvae, which hatch from the egg and devour woolen clothes before pupating. On the other hand the silkworm moth[13] is valued for the silk unwound from the cocoon in which the larva pupates.

[8] *Kallima paralecta.*
[9] *Porthetria dispar.*
[10] *Heliothis armiger.*
[11] *Carpocapsa pomonella.*
[12] *Tinea pellionella.*
[13] *Bombyx mori.*

Diptera. — The Diptera are an equally large order, composed of insects with a single pair of wings attached to the mid-thoracic segment, while the third segment bears a pair of knobbed threads which may represent vestigial wings. The mouth-parts are used for sucking, and metamorphosis is complete. In this order we find mosquitoes, gnats, midges, flies of all kinds (Fig. 187 *L*), and some degenerate parasitic types which have lost the wings.

The mosquito lays its eggs on water, often in masses known as rafts. The larvae live in the water but breath air through a tube on the abdomen. These wrigglers, as they are called, are easily killed by covering the water with a film of oil through which the wriggler cannot thrust its air tube and so perishes of suffocation. The female mosquito alone sucks the blood; the male, which is generally larger, lives on plant juices. The genus *Anopheles* transmits human malaria, whereas the common genus *Culex* does not transmit human malaria but a similar parasite which causes malaria in birds. A third genus, *Stegomya*, transmits the causative organism of yellow fever.

The house-fly[14] is now recognized as a harmful as well as an annoying form. Flying from exposed drains to the table, it carries the germs of typhoid fever and other diseases. Its eggs are laid in decomposing organic material of all sorts, especially horse manure. The larva is a worm-like organism known as a maggot. This secretes a tough membrane within which it pupates. The adult fly emerges in about twelve days after the egg is laid, so that many generations are passed through in the course of the summer. The fruit-fly, *Drosophila*, is a favorable object for genetic research because of the rapidity with which the fly reproduces. This genus lives on the yeasts encountered on the surface of fruits.

Among the parasitic diptera are the sheep-tick,[15] not to be confused with the cattle-tick,[16] already mentioned, which possesses four pairs of legs and belongs to the Arachnida. Another group of degenerate diptera are the fleas,[17] some of which are peculiar to man. The fleas proper to cats and dogs, however, are often found on unwilling human hosts, and the rat flea is suspected of transmitting bubonic plague from rodents to humans.

Coleoptera. — The Coleoptera (Fig. 187 *F*) or beetles have four wings, of which the first pair are sheath-like covers under which

[14] *Musca domestica.*
[15] *Melophagus ovinus.*
[16] *Boöphilus annulatus.*
[17] *Pulex irritans.*

the membranous hind wings are folded. The mouth-parts are biting, and metamorphosis is direct.

In this order are found carnivorous aquatic and terrestrial beetles, scavengers, and leaf-eaters. The tumble-bug is an American representative of the group to which the sacred scarab of the ancient Egyptians is assigned. It is seen rolling along a ball of dung in which the egg is laid and on which the larva feeds. The lightning-bug or fire-fly and the blundering June-bug are both beetles, as are the lady-birds, which feed on plant aphids and scale insects. The cotton-boll weevil belongs to this order.

Hymenoptera. — The final order of insects is the Hymenoptera, a group including among other forms the bees, wasps, and ants. These have four membranous wings, with relatively few veins. The mouth-parts are biting and sucking. The first segment of the abdomen is fused to the thorax. Metamorphosis is complete.

The bees show all gradations between solitary forms and colonial types. Thus the leaf-cutting bee lines cavities in wood with the leaves she cuts, deposits nectar and pollen for the developing young, lays her eggs, and flies away. The carpenter-bee, also a solitary form, watches and feeds the young. The mining-bees dig tunnels, sometimes close together, sometimes opening off a common main shaft. The bumblebees form colonies of which all but the young queens die in the fall. The queens survive to lay eggs from which a new colony is formed in the spring. The honey-bee,[18] as is well known, forms permanent colonies. There are three classes of bees, the queen or fertile female, the drones or males, and the sterile females or workers (Fig. 99). The male (see Chapter VI) develops from parthenogenetic eggs, whereas the queen and worker arise from fertilized eggs. Three different types of cells are constructed of wax, in one of which the parthenogenetic drone eggs are laid, another receives fertilized eggs which will develop into workers, while a third, the largest, receives the fertilized eggs which will develop into queens. The larvae hatch out into the bee-milk, a mixture of digested honey and pollen. They are fed this for several days, after which the worker and drone larvae receive undigested honey and pollen while the queen larvae are fed on the richer food until they pupate. The drones and queens are solely concerned with the reproduction of the colony, while all other activities are performed by the workers, who build the comb

[18] *Apis mellifica.*

from wax which is secreted in the wax glands. They collect pollen and nectar, which is evaporated down to honey, as well as **propolis,** a resin collected from trees and used for strengthening the parts of the hive (bee-glue), and water. They also feed and nurse the larvae and the queen, clean the hive, ventilate it by vibrating their wings, guard it and apparently provide new queen cells when the colony is becoming overcrowded. The new queen either battles the old until one is killed or gathers up a few thousand workers and swarms away to start a new colony. The anatomy of the bee shows a wonderful variety of structures developed on the legs of the workers by means of which these varied activities are carried on, but the reader is referred to books on Zoölogy or Entomology for these details.

The wasps too show a variety of stages between the solitary life of digger-wasps and the social life of the yellow-jackets, a species which constructs elaborate paper nests from wood-pulp. One of the solitary wasps has been observed using a stone to pound down the earth above its eggs, a unique example of tool using in insects.

But the social life of insects culminates in the highly organized ant colony, which may contain as many as a half million individuals. Among the ants (Fig. 187 *B, C*) four castes are often distinguishable, the males, females, workers, and soldiers. The males and females are originally provided with wings, but after the nuptial flight, from which only the females return, these pull off their wings and take up the task of laying eggs. The soldiers are usually characterized by a larger head, and their sole tasks are to guard the colony or the workers when these are out on fatigue duty, or again, to take part in raids on alien colonies. Some of these raids result in the taking of prisoners, for some species of ants are slave-holders and have even lost the power of feeding and cleaning themselves. Others are peaceful agriculturists who keep domestic animals or cultivate fungi. The "cow" of the ant is a species of aphid which secretes a sweetish liquid which the ants devour. The ants keep the aphids of the corn root in their nests over the winter (Fig. 123), but in the spring carry them through tunnels to the roots of the freshly sprouted corn. The leaf-cutter ants carry bits of leaves, held over the head like umbrellas, to their nests where others pack them into balls in a subterranean hothouse, and plant in these the spores of a fungus.[19] So important is this to the ants, that the queen who

[19] *Rozites gongylophora.*

leaves to found a new colony carries with her a supply of the spores in a pocket just below her mouth. The amazing honey-pot ant has a worker caste which distend themselves with honey until the abdomen is spherical and the exoskeletal rings are widely separated and then suspend themselves from the roofs of their underground storehouses through the winter. From time to time they are taken down and regurgitate their honey to other workers. We have spoken of the solitary wasp which was seen using a stone as a mallet. Among the ants there is a species which builds its nest of leaves, one " gang " of workers holding two leaves together while another, carrying the pupae, squeeze from them a silky material which glues the leaves together. We leave the ants with regret; volumes have been written concerning their social organization. It is difficult for us to believe that their actions may not be intelligent, that is to say, conditioned or educated. But the specialists agree that these are only elaborate instincts or chain reflexes. Certainly the little creatures have some way of communicating with each other, as they appear to guide or direct others towards some newly discovered source of supply.

The insects are so specialized in food habits that they are successful in placing a species in almost every niche of every biological association. Although they are typically land animals, yet we see in the aquatic larvae, particularly in those of the lower orders, traces of their origin from water-living ancestors. By virtue of their rapid development and powers of locomotion they spread over and occupy new territory with sometimes devastating speed. Their participation in the dissemination of disease and their attacks on domestic plants and animals have resulted in the wide-spread feeling that man's principal competitor for the dominance of the earth is the insect. This group, in spite of the size limits imposed by the chitinous exoskeleton, has by the development of so many highly specialized species successfully exploited every ecological field. The size range of insects lies between the microscopic parasitic wasps, which develop inside the egg of other species, to the Goliath beetles (six inches in length) and bird-eating spiders.

CHORDATA

All the phyla so far mentioned are often grouped as the invertebrates to distinguish them from the vertebrates, which like the frog are characterized as bilaterally symmetrical coelomate

animals with an internal locomotor skeleton, based on an axial series of bones known as vertebrae.

Protochordates. — But there are found a few invertebrate animals which lack a vertebral column and have in its place its precursor, an axial rod of elastic connective tissue known as the notochord. They also possess slits in the pharynx opening to the exterior, and a dorsal nerve cord. The latter it will be remembered is ventral in Annelida and Arthropoda. Because of these three characteristics, which are true also of the vertebrates in the

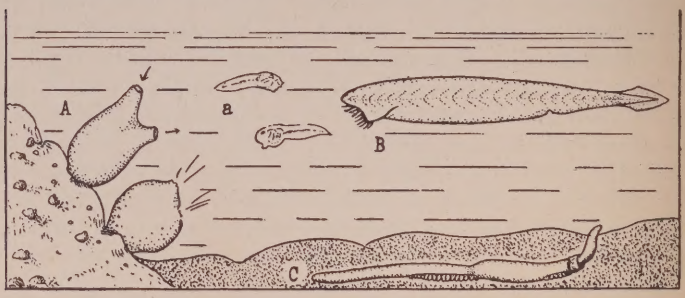

FIG. 188. — Protochordates. A, tunicate, expanded and contracted; a, free-swimming larvae of same; B, *Amphioxus*, C, *Balanoglossus*. (From Curtis and Guthrie.)

embryonic or adult condition, these aberrant forms are classed with the vertebrates in a phylum known as the **Chordata,** and they themselves are called protochordates. They include marine worm-like forms, e.g., *Balanoglossus* (Fig. 188 *C*), with a planktonic **tornaria** larva much like that of the echinoderms; marine mollusc-like forms, the **Tunicata** (Fig. 188 *A*), whose larvae (Fig. 188 *a*) possess a notochord lost in the adult; and a curious fish-like marine sand-digger, the lancelet *Amphioxus*[20] (Fig. 188 *B*).

Origin of the Vertebrates. — The origin of the vertebrates is lost in obscurity. All the invertebrate phyla are known from fossils in the Cambrian and even in some cases from pre-Cambrian rocks. The first vertebrates date from the next (Ordovician) period. There are three theories as to the ancestor of the vertebrate stock — first that it was some worm which took up a predacious habit, swimming upon the back. A second holds that the peculiar tornaria larva links the vertebrate stock with that which gave rise to the echinoderms. A third reasons that the Ordovi-

[20] Now known as *Branchiostoma lanceolatus*.

cian vertebrates, to which we shall turn presently, most resemble an extinct group of arachnids related to the king-crab *Limulus*

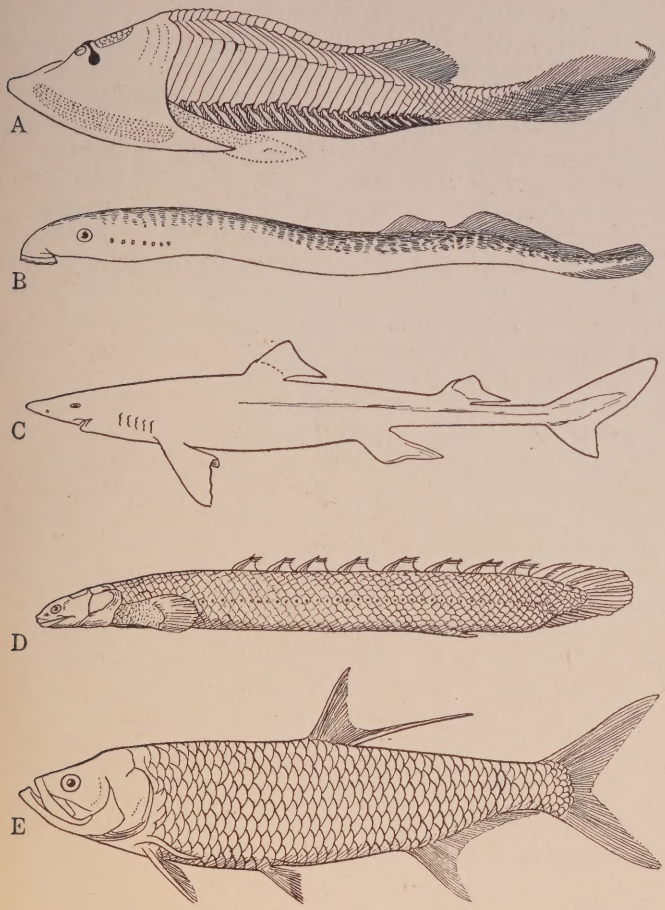

FIG. 189. — Fish. A, *Cephalaspis*, an extinct armored fish, (after Patten); B, *Petromyzon*, the lamprey (after Parker and Haswell); C, *Squalus acanthius*, the spiny dogfish (after Dean); D, *Polypterus bichir*, a fringe-finned ganoid (crossopterygian) (after Bridge); E, *Megalops atlanticus*, the tarpon, a giant teleost (after Goode).

and flourishing in Cambrian and Ordovician days, and that therefore the ancestor is to be found among the arthropods.

Ostracodermata. — The first vertebrates are peculiar armored fish known as the Ostracodermata. Many of the fossils originally assigned to this group have recently been transferred to the true fish, and those which remain are characterized by the possession of three pairs of jaws and a single pair of jointed appendages borne on a fused cephalothorax. *Cephalaspis* (Fig. 189 *A*) is an example of one of the later members of this group (Devonian).

Cyclostomata. — The most primitive living vertebrates are found in the class Cyclostomata or round-mouth fish. These lack true jaws and are ectoparasitic on other fish. Two groups are distinguished, the lamprey eels (Fig. 189 *B*), found in fresh and salt waters, and the exclusively marine hagfish. Neither has teeth on the jaws, but horny outgrowths on the tongue serve as rasping organs by which they eat their way into their prey. They lack paired appendages, swimming by snake-like undulations, and the skeleton is entirely cartilaginous.

Chondrichthyes. — The third class of vertebrates is that made up of fish with two pairs of jaws, two pairs of appendages used as fins, and a cartilaginous skeleton. These cartilage-fish are called Chondrichthyes. They are found in the Silurian and later periods, and they dominated the marine life of the Palaeozoic. Today they are represented by the sharks (Fig. 189 *C*), skates, and chimaeras. To the embryologist they are interesting because the female lays relatively few eggs, but these are provided with chitinous shells and large amounts of yolk. Sometimes the young are retained within the oviduct, and the yolk-sac, after the contained yolk is consumed, is pressed against the oviducal wall to act as a pseudo-placenta whereby maternal secretions can be utilized as food for the embryo. Such an organ is not found again until in some of the viviparous reptiles and mammals. Anatomically the sharks and their allies (**Elasmobranchii**) are quite primitive, and the study of vertebrate zoölogy often begins with the dissection of the dogfish. Among other curious things about the cartilage-fish are their scales, which are called **placoid** scales and resemble thorns with a bony base and are encased in a shiny hard layer known as enamel. The teeth of higher vertebrates are apparently derived from this type of scale which lines the skin over the jaws as well as outside the body.

Osteichthyes. — The remaining class of typically aquatic vertebrates is composed of the bony fish or Osteichthyes. This group shows a transition from ancient forms in which cartilage was only partially replaced by bone (the **ganoids**), now repre-

sented by a few species, mostly in the Mississippi river and the Nile, to the highly varied and numerous species of modern fish (the **teleosts**). These first appeared in the Jurassic period and now number over 10,000 species, fresh-water and marine. Space will not permit more than the mention of some of the more peculiar forms such as the flying fish *Exocoetes*, which glides through the air with the aid of its wing-like pectoral fins. A few have even become partially adapted to air breathing, like the climbing perch.[21] The food fishes of the sea and the fresh waters play an important part in the potential wealth of the nation, and game and ornamental fish add much to the pleasures of life.

Two of the archaic groups, however, demand special mention because they have been considered in or near the ancestry of the terrestrial vertebrates: the **Dipnoi** or lungfish, and the **Crossopterygii** (Fig. 189 *D*) or fringe-finned ganoids. The first group, which attained its climax in point of numbers during the Devonian period, is represented today by four species scattered in the relatively inaccessible branches of the Nile and the Amazon. They are remarkable in view of the fact that, when the waters become foul, before actually drying up, the fish use their air-bladders as lungs, gulping down air which is respired through the capillaries of the air bladder. The structure of their paired fins, however, would appear to bar them from the direct line of ancestry. Some of the Devonian Crossopterygii, e.g., *Eusthanopteron*, have a fin the bones of which are arranged approximately in the order characteristic of the tetrapods, as the forms above the fish are called.

Amphibia. — It is the Devonian rocks which contain the first indubitable evidence of the existence of tetrapod vertebrates in the form of a single footprint which has been assigned to an unknown animal *Thinopus*. In the following periods which are collectively called the Permo-Carboniferous, in which our great coalbeds were formed, there are found the skeletons of many varieties of four-footed animals which appear to belong to the Amphibia (Fig. 190 *B*).

This class of vertebrates is distinguished by the fact that the appendages are five-fingered (typically), and that the skin of modern examples is not protected by scale, feather, or hair. They have never become completely adapted to terrestrial life, as the eggs must be laid in water and pass through a fish-like larval stage known as the tadpole. The more primitive amphibia possessed a tail, and in this respect the order **Anura** to which

[21] *Anabas scandens.*

the frog belongs is more specialized. The newts and salamanders, the water-dog *Necturus* (Fig. 190 *A*), and other caudate forms resemble the ancient types more nearly. Some amphibia like *Necturus* spend all their life in the water and breathe throughout their life by external gills. Others like the newt *Eurycea* respire exclusively through the richly vascular moist skin. The

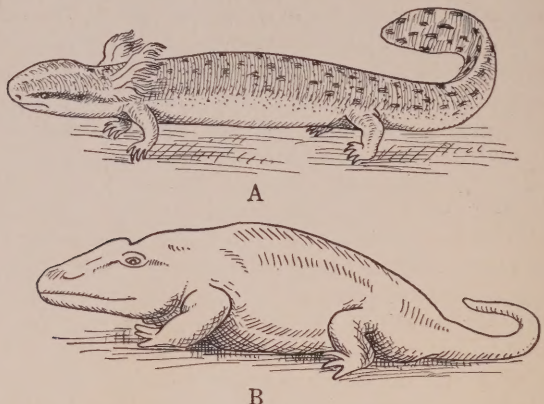

Fig. 190. — A, *Necturus maculosus*, a tailed amphibian with permanent external gills (after Newman); B, *Eryops*, an extinct amphibian of the Palaeozoic (after Romer).

African hairy frog *Astylosternus* is distinguished by a rich growth of hair-like dermal processes about the thighs which serve as accessory breathing organs. There are burrowing species, the legless blindworms, and arboreal forms, e.g., the tree-toad. But the group today is the smallest in point of numbers of any vertebrate class. Few of the modern forms are over six inches in length, although the giant salamander of Japan may grow to four feet, but many of the extinct forms were over six feet in length.

Reptilia. — During the latter part of the Permo-Carboniferous, the climate of North America changed from a tropical to almost a glacial type, and the archaic amphibian fossils were replaced by those which the specialist recognizes as those of reptiles. The modern reptiles are distinguished by the possession of scales, so that even an amateur can distinguish between a scaly lizard and a naked salamander or between a scaled snake and a smooth-skinned blindworm, but few apparently do so. The internal

characters differ markedly, however, so that a study of the skeleton will serve to place all but a few intermediate groups into either amphibia or reptilia.

During the Mesozoic Age the reptiles reigned supreme, and nearly thirty orders are distinguished in the class of which only four survive today. There were dragons in those days, dragons of the air, the leathery-winged **Pterodactyls** with a wing spread of nearly twenty feet, dragons in the water, the armored **Plesiosaurs** and **Ichthyosaurs,** and dragons on the land, the **Dinosaurs.** This last group (Fig. 191) included the largest vertebrates that

Fig. 191. — Restoration of a dinosaur, *Ceratosaurus,* devouring the flesh of some herbivorous reptile. (After Lucas.)

ever trod the earth. Some were herbivorous, such as the mighty *Brontosaurus,* nearly eighty feet in length from snout to tail-tip, and having an estimated weight of forty tons. Such a beast could only have lived partly in the water, whose buoyancy could assist the massive legs in bearing such a weight. Others were carnivores and preyed upon the great herbivores, as did *Tyrannosaurus,* which stood twenty feet in height and whose ferocious jaws bore teeth six inches in length. Most of the carnivores were bipedal, and some had skeletons of such slight proportions that it is believed that they preyed upon the clumsy birds which are first discovered in the Jurassic. Aside from the skeletal remains of the dinosaurs much can be learned from a study of their footprints which are often preserved in rocks of the Triassic which once represented great mudflats. Recent explorations in Mon-

golia have brought to light the fossil eggs of one species of dinosaur so well preserved that the skeleton of the developing young may be worked out. Why this once dominant race became extinct no one knows. Some have imagined that it was due to climatic changes through which the food supply became reduced. Others find significance in the fact that towards the end of this age the insects were flourishing and may already have commenced to harbor disease-causing parasites. Still others note the appearance of tiny mammals which like some of the modern types might have sought out the eggs of the great beasts, and thus brought about their downfall for like all large animals the dinosaurs presumably had a slow rate of reproduction.

The modern reptiles include the turtles and tortoises, snakes and lizards, the crocodiles and alligators, and the curious *Sphenodon* (Fig. 192 *D*), sole surviving representative of an ancient Mesozoic order. This species, found only in New Zealand, has among other strange characteristics a median third eye on the top of the head, a feature not uncommon among the amphibia and reptiles of the Permo-Carboniferous. Some forms of large size are still found, the giant sea-tortoise of the Galapagos Islands (four hundred pounds), the boa-constrictor (thirty feet), the strange carnivorous lizards of Borneo, and alligators which attain a length of fourteen feet.

Most modern reptiles have taken up an aquatic life, although turtles, some snakes and crocodiles are terrestrial, and chameleons and some other lizards are arboreal. There is one so-called flying lizard *Draco,* whose expanded ribs bear a loose fold of skin by means of which the animal glides or rather parachutes down from treetops. The reptiles show their most marked advance over the amphibia in their dependence upon air breathing and the consequent partial separation of the vascular system into a pulmonary division (to the lungs) and a systemic division (to the rest of the body). Finally they have, with the exception of *Sphenodon,* copulatory apparatus by which the fertilization of the egg is accomplished inside the body of the mother, and the egg protected by a shell is laid on land. With this goes the development of extra-embryonic membranes by means of which the life of the embryo within the shell is facilitated. Some reptiles are called viviparous, but in all cases eggs with shells are formed and retained within the body of the mother until after hatching. The shells of reptiles' eggs are generally uncalcified, but those of the snapping turtle have a thin coating of calcium carbonate.

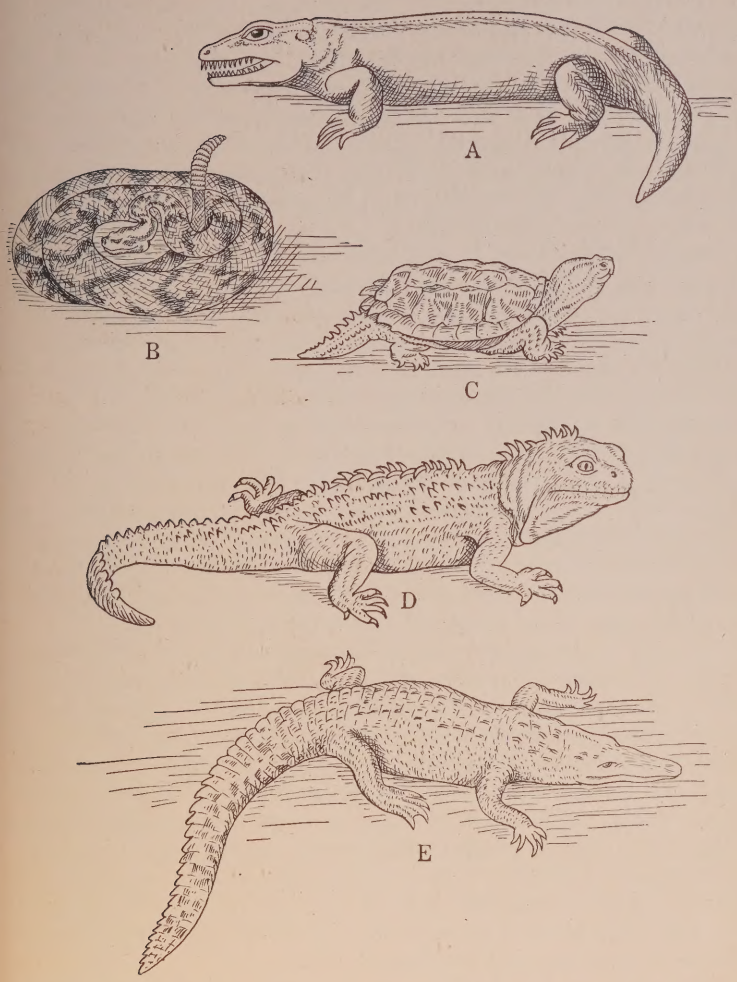

FIG. 192. — Reptiles. A, *Seymouria*, an extinct reptile of the Permo-Carboniferous (after Williston); B, *Crotalus durissus*, the rattlesnake (after Lydekker); C, *Chelydra serpentina*, the snapping turtle (after Lydekker); D, *Sphenodon punctatum*, a modern survivor of an ancient stock (after Gadow); E, *Crocodilus americanus*, the alligator (after Ditmars).

The remaining classes, the birds and mammals, show a marked advance over the reptiles in that they have developed temperature-regulating mechanisms by which the temperature of the body may be kept above that of the surrounding air or water. For this reason they are popularly known as the warm-blooded vertebrates. Although the bodily activities of the amphibians and reptiles are largely dependent upon the temperature of their surroundings, these groups are more independent of climatic conditions.

Aves. — The Aves, as the birds are called, are distinguished by the fact that the first pair of appendages are modified to serve as wings, the bones of the skeleton are hollowed and many contain air sacs, or extensions of the lungs, and that the body is covered with feathers, with the exception of the lower legs which are scaly. The general anatomy of the bird is much like that of the reptiles, so much so that Huxley once said that the birds were only glorified reptiles. Point was lent to this saying by the discovery of a Jurassic fossil of a creature that was reptilian in the possession of teeth, claws on both arms and legs, and a long reptilian tail, but avian in the development of wings and the fact that the body was clothed in feathers. *Archaeopteryx*, as this strange creature is called, has already been mentioned (page 231) as an example of a palaeozoölogical missing link.

Several of the Cretaceous birds possessed teeth, but modern forms are entirely toothless although their embryos show traces of the germs of teeth. There were many birds, like the South American *Phororachis*, which abandoned flight, as has the ostrich today, and developed great speed of limb. This giant bird was carnivorous and as dangerous to the early mammals as is the great owl or hawk of today to their modern descendants. The birds, like the teleost fishes and the mammals, are latecomers on the globe and are in the heyday of their development. About 12,000 species are known, strictly terrestrial, arboreal, aquatic, littoral, or even burrowing in habit. The special study of birds is known as **Ornithology.**

The conquest of the air by the birds permits of extended seasonal migrations, so that flights from tropical to arctic regions and vice versa are not uncommon. With their ability to withstand temperatures far lower than those necessary for the continuance of vital activities, because of their powerful muscles developing heat, and the efficient coat of feathers acting as insulating agents, the birds are able to exploit the arctic regions,

which are closed to cold-blooded types such as the amphibians and reptiles. During the arctic winters they may fly to warmer climes, while mammals whose powers of locomotion are more limited are forced to long periods of hibernation. The number of young produced by the birds is smaller than in most groups so far studied, but there is a larger amount of parental care. The nesting habits of birds, the part played in incubating the eggs, the parents' habit of bringing food and often partially digesting it, and what seems to be the training of the young in flying and obtaining food all represent a great advance in social evolution. Many birds mate but once, it is believed, and a great many display elaborate "courting" phenomena at the onset of the breeding season. The males and females differ markedly in plumage, and experiments seem to indicate that this secondary sexual character is the direct result of endocrines secreted by the gonads, for castration or the removal of the gonad often brings about a reversal of secondary sex characters. In this connection it should be mentioned that recently a few cases have been recorded of birds actually changing their sex during their lifetime — a phenomenon for which no adequate explanation has yet been offered. The size range of birds extends from the South African ostrich which stands over eight feet and weighs over three hundred pounds down to the tiny humming-bird no larger than a good-sized insect and with a weight of two grams. Most birds weigh very little for their size, as would be expected.

Mammalia. — The mammals are distinguished from the other classes by the presence of hair, mammary or milk glands, and a diaphragm which augments the respiratory power. The class Mammalia is divided into three subclasses, according to the amount of prenatal care accorded the developing young. The first group are known as the **Prototheria,** or egg-laying mammals. Only a few species survive, in Australia, New Guinea, and Tasmania. The anatomy of the egg-laying mammals resembles the reptiles in many respects, particularly in that the oviducts do not unite to form a uterus and vagina but open separately into the cloaca, so that there is a single urogenital aperture or vent. The mammary glands too are not localized into definite mammae or breasts but scattered over the ventral surface and indicate their evolution from sudoriparous or sweat glands. It is quite possible that these strange creatures represent rather specialized descendants of the tiny mammalian creatures which appeared in late Mesozoic time. They are specialized in food habits, for

FIG. 193. — Mammals. A, *Phenacodus primaevus*, a Cretaceous type (after Osborn); B, *Ornithorhynchus anatinus*, the duckbill, an egg-laying mammal (after Vogt and Specht); C, *Trichechus latirostris*, the manatee, a marine ungulate, possibly the source of the legend about mermaids (after Vogt and Specht); D, *Petrogale xanthopus*, a kangaroo, one of the marsupial mammals (after Fuertes).

two genera, *Echidna* and *Proechidna*, are ant-eaters, and the duckbill, *Ornithorhynchus* (Fig. 193 *B*), has a duck-like bill with which it searches the mud for worms and insect larvae. *Echidna* has one interesting habit which foreshadows the next group in that the female picks up the newly laid egg with her mouth and places it in an abdominal pouch in which hatching takes place.

The mammals have definitely taken the place of the reptiles as the dominant land vertebrates during the Tertiary period. The clumsy archaic mammals (Fig. 191 *A*) of the Cretaceous and Paleocene are replaced by the precursors of modern species. Alone in Australia there persists the remnant of an ancient tribe, the **Marsupialia,** a subclass characterized by the fact that the young although retained and nourished for a time in the uterus, are born long before development is complete. They crawl or are placed by the mother in a pouch on the abdomen (Fig. 193 *D*), where they glue themselves to her nipples and remain until able to move about for themselves. The kangaroo when born is but a scant two inches in length, the eyes are still incapable of opening, and the very fingers and toes are not yet formed. Australia has a fauna which is exclusively marsupial so far as the mammals are concerned, and every ecological position is occupied by a marsupial. The large herbivores are kangaroos, there are dog-like and cat-like marsupial carnivores, flying phalangers like squirrels, and a koala which is for all the world an animated Teddy bear. Students of faunistic geography explain this marsupial stronghold as due to continental movements by which Australia was cut off from the other continents after it had been populated by an archaic marsupial stock but before any of the modern placental mammals had arrived. Very few marsupials are found in other continents. The United States has only the opossum.[22]

Placental Mammals. — The remaining mammals belong to the subclass **Eutheria** in which the young are nourished in the uterus by means of a foetal appendage, the placenta, an organ of exchange in which the blood of the mother and the developing young are placed in close juxtaposition. No actual exchange of blood takes place, but food in solution and oxygen and carbon dioxide pass from one blood stream to the other in an absorptive process concerning which too little is known.

From the time of the Eocene, the lines of descent of many modern mammals have been worked out in the same way, but without quite the wealth of detail, as that of the horse. A large

[22] *Didelphys virginiana.*

number of orders are recognized, but these may be grouped into four superorders, the **Unguiculata** with claws on the ends of the digits, the **Primates** with nails, the **Ungulata** with hooves, and the **Cetacea** whose appendages have become flippers adapted to marine life.

Unguiculates. — The Unguiculata include the most primitive or generalized of the modern mammals, the insectivores or insect eaters, such as the hedgehog (not to be confused with the porcupine, which is a rodent), the mole, and the shrew. They are distinguished by their sharp-pointed teeth. The bats are a related group in which the anterior appendages are modified for flying. These like the insectivores are nocturnal creatures which are principally insectivorous, although some varieties are fruit eaters, and others, the vampires, suck the blood of larger mammals. Between these groups come the flying lemurs of the Philippine Islands. The carnivores are divided into the two groups of the terrestrial forms including the dogs, cats, and other flesh eaters, and the marine seals and walruses. Here too are placed the gnawing rodents, all herbivores, including the rabbits, squirrels, mice, guinea-pigs, and the porcupine. These can always be distinguished by the chisel-like incisor teeth which grow throughout life. Another group of the unguiculates are characterized by the absence of enamel on the teeth and the partial loss of the teeth themselves. These edentates are mostly South American and include ant-eaters, the vegetarian sloths, and the insectivorous armadillo, which crosses the Rio Grande and ranges through lower Texas. The scaly ant-eater of Africa and Asia and the South African Aard Varks, also ant-eaters, belong to closely related orders.

Ungulates. — The Ungulata or hooved mammals are exclusively vegetarians, although the pig is practically omnivorous. Here belong two great groups separated by the fact that the toes are even or odd in number. Students of mammalian evolution explain the origin of both from five-toed ancestors by the difference in the position of the feet in running. All cursorial mammals are distinguished by their length of limb usually attained by running on the tips of the fingers or toes. Place your hand on the table palm down, exactly as you stand on the sole of the foot. If the entire hand touches the ground as you raise or lower it, this is typical of what is called **plantigrade** locomotion. Now lift the palm but allow the fingers to remain touching the table for their entire length. This illustrates **semi-digitigrade** locomotion.

Now raise the fingers slowly while allowing the tips to touch the table. This is called **digitigrade** locomotion. You will notice if the hand is raised straight forward we pass through a stage in which five, four, three fingers and finally only the middle finger touch the table. This is the line taken by the **Perissodactyls** such as the horse, rhinoceros, and South American tapir. If on the other hand the fingers are toed in slightly, we pass from a four-fingered to a two-fingered stage characteristic of the **Artiodactyls,** pigs, peccaries, hippopotami, and the ruminant or cud-chewing camels, their South American relatives the llamas and guanacos, the giraffes, deer, sheep, cattle, etc. Other ungulates are the two species of elephants, Asiatic and African, with plantigrade locomotion, which with their recently extinct relatives the mammoths and mastodons include the largest terrestrial mammals. Here also are included the herbivorous marine sea-cows or manatees (Fig. 193 *C*), whose heads, lifted above the surface as the females held the young folded in their flippers, may have given rise to the legends of the mermaid. The biblical coney too is an ungulate and apparently most nearly related to the elephant stock.

Cetaceans. — The Cetacea or whales and porpoises are supposed to descend from terrestrial carnivores. They have become completely adapted to marine life in that the limbs are modified to serve as fin-like paddles, and the tail has become flattened sideways as a propeller. The skin has a thick layer of fat by means of which the cetacean preserves its body heat. Most of the hair is lost, and the whales have only a few bristles around mouth and nostrils. The young are borne in the uterus until well grown and thereafter suckled at the breast as are other mammals. Two orders are distinguished, the toothed whales and the whale-bone whales. In the latter the teeth are lost and the jaws bear great sheets of baleen, whale bone, through which the whale filters the water and retains the plankton on which it feeds. Some whales attain enormous size. The sulphur bottom,[23] as the whalers call it, reaches a length of nearly a hundred feet, a weight of three hundred thousand pounds, and is the largest mammal alive or extinct.

Primates. — The Primates, or mammals with nails on the ends of the fingers, include the lemurs, monkeys, apes, and men. The early primates show many affinities with the insectivores and may well have arisen from a common early placental stock. The

[23] *Balaenoptera sulphureus.*

members of the group show evidences of passing through an arboreal stage in evolution, and many lemurs, monkeys, and some apes are still primarily tree dwellers. In the anatomy of the body the primates are not nearly so specialized as are the ungulates and cetaceans, and they are allowed to retain the position of primacy given them by Linnaeus only because in this group is seen the highest evolution of the brain.

Evolutionists tell us that this is due originally to an arboreal life, in which the arms were freed from purposes of locomotion and used for grasping first the boughs of trees, then food and finally implements. Curiosity is characteristic of monkeys and apes, and the latter particularly may be taught the use of implements. The apes resemble man in so many points of their anatomy that they are placed in a common suborder, the **Anthropoidea,** and many students of mammalian evolution consider that they arose from a common ancestor. Professor H. F. Osborn, on the other hand, maintains that the two stocks were separated almost from the beginning of Eocene times and may have arisen from different members of the insectivore-primate ancestral stock.

Man. — If this should be so, the two races must have evolved along remarkably similar lines, and most palaeontologists consider that the separation of the ape family (**Simiidae**) and the human family (**Hominidae**) took place not earlier than the boundary between the Oligocene and Miocene. The first fossil remains which can be placed in the human family are those of the Java man[24] (Fig. 194 *A*), long known as the "missing link." Discovered by a Belgian army surgeon, Eugene Dubois, in 1891, the remains were studied by a congress of anatomists who found them intermediate between those of men and apes but showing on the whole more human characteristics than ape-like. In the Pleistocene quite an array of human species ("fossil men") are found. The dawn man of Piltdown, England (*Eoanthropus*), (Fig. 194 *B*), a similar Chinese skull, a skull from Rhodesia in Africa, the Heidelberg man of Germany are all solitary evidences of the existence of semi-humans who ranged the world in the various interglacial periods of the Ice Age. In the latest of these interglacial periods a race inhabited Europe and left not only buried skeletons but stone implements, through the study of which a great deal of information concerning this Neanderthal[25] (Fig. 194 *C*) race has been deduced. They were

[24] *Pithecanthropus erectus.* [25] *Homo Neanderthalensis.*

succeeded by a distinctly human and highly advanced race of Cro-Magnons[26] (Fig. 194 *D*), the last of the men of the Old Stone Age, as the makers of unpolished stone (**palaeolithic**) implements are called. Yet it must be recalled that when the Americas were first discovered by Europeans the greater part of North America was inhabited by Indians whose culture was decidedly palaeolithic.

The men of the Old Stone (Palaeolithic) Age were succeeded by races which made use of polished stone implements, known to

A B C D

FIG. 194. — Extinct races of men. From left to right, *Pithecanthropus, Eoanthropus* (the Piltdown man), the Neanderthal man, and the old man of Cro-Magnon. (Photograph by courtesy of the American Museum of Natural History. For that of the new *Pithecanthropus* bust, I am indebted to Prof. J. H. McGregor.)

archaeologists as men of the New Stone (**Neolithic**) Age. This period was succeeded by the Bronze Age in Europe, and this in turn by the Iron Age. These latter ages blend into the time of recorded history.

The study of man from the biological point of view is known as Anthropology and has two major divisions, the study of the human body, Physical Anthropology, and the study of the artifacts (cultural implements) made by man, Archaeology. But the boundaries separating Archaeology, Physical Anthropology, Ethnology (study of primitive customs), Linguistics (study of primitive languages), and the social sciences in general are exceedingly tenuous. The data drawn from all must be synthe-

[26] *Homo Cro-magnonensis.*

sized if we are ever to attain even the faintest conception of the origins and migrations of the human strains, which, almost inextricably interwoven, inhabit the earth today. Anthropologists distinguish some 26 varieties of the modern man (*Homo sapiens*). These are grouped into three main divisions: (1) the **Caucasian** or white race, (2) the **Ethiopian** or black race, and (3) the **Mongolian** or yellow race. The red man or **Amerind** is generally held to be a Mongolian variety.

Summary. — Our all too brief survey of the course of animal evolution has led us from the single-celled protozoa to the two-layered coelenterates and thence to the three-layered animals. Some of these developed a body cavity but diverged along other lines. The echinoderms lost their original bilateral symmetry in connection with a sessile life. The molluscs while retaining their bilateral symmetry developed a protective external skeleton and largely abandoned the power of rapid locomotion. The annelids developed a segmented body. Some of these became arthropods by the assumption of a jointed external skeleton which combined protection with locomotion but thereby limited their power of growth. From one of these stocks came the chordates with pharyngeal gill clefts, an internal supporting notochord, and dorsal axial nervous system.

Among the chordates the fish are first to be found in the geological record. Some of these emerged early in the Devonian as the first clumsy amphibians. From this stock a race arose whose eggs could develop on land, and these, freed completely from the water, were the first reptiles. Certain strains of reptiles developing thermo-regulatory mechanisms gave rise to the birds and mammals. From the latter strain came the first placental mammals, and from some insect-eating line of these the primate stock arose. The arboreal habit released the hand from use in locomotion, and the brain, especially the cerebrum, increased in size and complexity when the human race left the trees.

These primitive men slowly won to speech and the use and manufacture of implements so that biological inheritance could be supplemented by education and material heritage. The evolution of man from this point has been a process extending over half a million years. During these few seconds of geological time he has developed from an inarticulate, semi-arboreal, ape-like beast to an educable social being who has covered the surface of the earth, delved deep beneath its surface, exploited the seas, is

conquering the air and bending all other organisms to his use. Concerning his mental life and in particular his peculiarly human attitude to those intangibles which we call spiritual values the biologists cannot apply his scientific measures and methods. But looking back upon the past, he regards the future with assurance that the evolutionary process has not yet come to an end.

CHAPTER XII

APPLIED BIOLOGY

Thomas Huxley, in his celebrated address on the meaning of a "liberal education," said, "Yet it is a very plain and elementary truth that the life, the fortune, and the happiness of every one of us, and, more or less, of all who are connected with us, do depend upon our knowing something of the rules of a game infinitely more difficult and complicated than chess." He referred, of course, to the game we know as life and to the rules which we call the principles of Biology.

MAN'S PLACE IN NATURE

In the web of life, man occupies a position which is, so far as he can see, unique, in that he alone has the power of thought. But thoughts can be expressed only in action, that is to say, through the activity of the body. For if we attempt to communicate our thoughts we can do so only by speech, gesticulation, writing, or some other action which involves muscular activity.

The human body, as the reader has doubtless realized long before arriving at this page, is that of a highly organized animal. Function by function, structure by structure, the human body may be compared with that of the frog and the two will be seen to correspond in a general way.

Our organ systems are specialized for digestion, circulation, respiration, excretion, the production of endocrines, sense perception, transmission and coördination, muscular contraction, leverage, and reproduction. The human body is made up of cells, and these manifest the same characteristics of metabolism, sensitivity, and reproduction as do the cells of other organisms.

Within these cells chromosomes are evident at times when mitosis takes place, and the number of chromosomes is reduced in the maturation of the germ cells. Individual characteristics (only a few, to be sure) are known to be transmitted in accordance with the Mendelian laws, and several examples of sex-linked inheritance have been demonstrated.

Ecologically, man has shown great powers of adaptation, and his entrance into natural communities has usually resulted in his attaining a dominant position. But the rules of the game apply to him fully. His animal nature makes him dependent upon the plant kingdom directly as a vegetarian, indirectly as a meat-eater. He competes with other animals for his food and either exterminates them, domesticates them to his use, or endures what he cannot subdue. He has conquered, to all intents and purposes, the predators of great size which preyed upon him when the world was young, but he still must fight the parasitic bacteria, molds, yeasts, protozoa, worms, and insects which attack his body, and that even more varied array of competitors which destroy his crops and the products of his civilization.

Historically, man is a product of the evolutionary process. Linnaeus long ago recognized man's resemblance to the apes and placed them together in the order Primates, elevated to the head of the taxonomic system by virtue of the included human species. Part for part the human body corresponds to that of the great apes with startling fidelity. At the present time professional palaeozoölogists are debating with great heat the problem of the exact relationship between the apes and man. Some hold that the relationship is quite close, and that the two stocks separated comparatively recently in geological time from a common ape-man ancestor. Others hold that the two stocks parted company much earlier, and that the resemblances are the result of both races taking up a similar arboreal mode of life (convergent evolution). But though biologists hope for a measure of accuracy even in historical matters, a few million years more or less are after all but a few minutes in cosmic chronology. The evidence from Palaeozoölogy, comparative Anatomy, and Embryology all indicates that man is a member of the animal kingdom, a vertebrate, mammal, and primate, and that even since the first appearance of the human stock he has undergone evolutionary change.

The evolution of the human race is not confined to the structure of the body alone but is shown also in the nature of the artifacts whereby the activities of the body are strengthened and diversified. Man as an organism is unique, further, in that he has learned to utilize instruments recording differences in measurement which his unaided sense organs cannot perceive. The use of glasses in daily life, of telescopes by the astronomer and microscopes by the biologist, and of the ultra-microscope and X-rays by chemists, has increased our vision far beyond the powers of

the human eye. The chemist can distinguish the presence, and analyze the constituents, of substances too diffuse to be detected by the nose or tongue. The radio picks up far-flung waves and transmutes them into sounds again perceptible to human ears.

So too have his responses increased in variety and power. His machines carry him to all parts of the world, build shelters and manufacture clothes, supply heat or cold at will, and produce with ever-increasing speed and efficiency all the objects which he considers necessary or pleasant in his daily life. Some are of almost unbelievable delicacy, performing automatic tests more sensitively than can the human mechanism. And most wonderful of all, he now constructs machines which build machines, and others which perform with speed intricate mathematical calculations.

But still the human body, which imagines and constructs the machine, is subject to the biological laws which govern its behavior and determine the duration of its existence.

MEDICINE, PUBLIC HEALTH AND HYGIENE

The study of the human body as a functional mechanism is the peculiar province of Medicine. Here the facts gleaned from the study of metabolism, irritability, and reproduction are applied directly to human life. The long study of the human body in health and disease has shown that its organization differs from that of the frog only in details.

The nutrition of man is holozoic in the sense that he can utilize manufactured food only, but within these limits he is omnivorous. The study of his food and its metabolism is covered in the sub-science Nutrition. The mechanism by which he digests his food is an elongate tube, with a muscular stomach and glands, including liver and pancreas, which secrete the digestive enzymes. His teeth are of the generalized primate type, and his vermiform appendix seems a vestige of the days when prehuman ancestors subsisted on a coarser diet.

The digested fraction is absorbed through the intestinal lining to circulate through the common carrier, the blood stream. The double circulation involving the shorter lung circuit and the longer body circuit are so separated that there is no mixture of aerated and non-aerated blood. Every part of the body is reached by capillary junctures so that food and oxygen are supplied to each cell and wastes and other secretions carried away.

The wastes are extracted through the kidney, lungs, and sudoriparous glands of the skin. The evaporation from the latter organs plays an important part in the thermo-regulatory mechanism of the body, as do also the expansion and dilation of the skin capillaries.

The blood as a common carrier maintains a constant hydrogen-ion content as well as an average percentage of certain inorganic salts approximately equivalent to that of sea-water three times diluted. Any considerable deviation in the percentages of the various blood constituents leads to metabolic disharmonies manifested in disease.

The endocrines play a very important part in human metabolism, and from the study of these (**Endocrinology**) there has arisen a fund of knowledge sufficient for skilled physicians to employ the endocrines as medicine (**Organotherapy**). The white blood corpuscles in the blood act apparently as scavengers. They can pass through the interstices of the cells making up the lining of the capillaries and to the seat (**focus**) of an infection where they attack the bacteria concerned. In the case of a wound, the leucocytes, dying, secrete a substance which activates the connective tissue cells to rapid division, whereby scar tissue is formed.

The clotting of the blood when a vessel is injured results from the actions of some of the proteins normally present in the blood serum. Other proteins known as **antitoxins** combine loosely with poisonous toxins liberated by pathogenic bacteria, as in diphtheria, or agglutinate the bacteria into motionless clumps where they can be destroyed by leucocytes, as in typhoid, or actually destroy the bacteria themselves.

Practically all the drugs which are used by physicians are carried in the blood after having been absorbed through the epithelium of the gut or injected directly into the circulation. But the discussion of drug actions would lead us far from our present subject, which is, in short, an attempt to indicate that the metabolism of the body is responsible for its normal activities.

This is particularly true of the behavior of man. His activities, aside from the secretions of the various types of glands, are essentially muscular. And the activities of the muscles are stimulated by nervous impulses exactly as in the frog and can be modified similarly. The involuntary muscles of the viscera are largely governed by the autonomic nervous system, and some physiologists hold that the peristaltic action of the intestine is controlled almost entirely by means of a nerve net not essentially different

from that of *Hydra*. The skeletal muscles, including those used in speaking and writing, are under the direct control of the central nervous system. The human brain is distinguished by the enormous development of the cerebrum, which contains nearly ten billion intermediate neurones with innumerable synaptic connections. Consequently the reflexes of man are seldom simple and usually involve chains of intermediate neurones which are present in such numbers that an almost infinite variety of response to external stimuli is possible. The complexity of the synaptic connections established through use and disuse (conditioning, education) is alone sufficient to account for the unpredictability of human behavior. The effect of the endocrines on the involuntary actions seems to be concerned with most if not all of those actions which we call emotional.

The physician is familiar with the mental and emotional responses to disturbances arising directly from disease or from drugs introduced into the body in its treatment. Many of the manifestations of abnormal Psychology may be traced to one or another of these causes.

Reproduction in the human race is entirely sexual and always syngametic. The differentiation between the sexes is well marked, and many secondary sexual characters are recognized. The embryo spends the first ten lunar months of its development within the body of the mother, and thereafter its normal nutrition for the first few months is obtained from the mother's milk. Sexual maturity is not attained until after a period of years, differing in various races and climates, and the reproductive ability does not persist throughout life, ceasing first in the female.

Disturbances in the reproductive system are often of far-reaching consequences because of the endocrines secreted by the genital glands and the effects of these in maintaining the endocrine balance. Hence mental and particularly emotional symptoms often follow in the train of diseases of this system. Many of the anomalies or structural abnormalities of the adult are due to irregular development during embryonic life, and a knowledge of the normal course of human Embryology is essential to an understanding of the normal anatomy of the human body. It is not possible in the limited space at our disposal to do more than indicate some of the ways in which Pathology, or the study of the body in disease, rests upon the examination of disturbances in metabolism, irritability, and reproduction. The application of

these laws to the activities of the human body is the peculiar province of Medicine, taken in the largest sense, and it is significant that the teaching in our great medical colleges is based on the foundations of Biology and Chemistry. Human Anatomy is best understood after a previous grounding in comparative vertebrate anatomy, and the study of human Physiology has been aided by a long series of experiments upon lower organisms. The precise and daring operations by which so many lives are prolonged are the results of countless operations on animals which would have been forbidden had the anti-vivisectionist propaganda been successful. Medical knowledge based on biological principles and applied to the life of the individual is sometimes called **Hygiene,** but when applied to the life of the human community it is known as **Public Health.**

In the preceding chapters it has been stated that bacteria, molds and yeasts, protozoa, flatworms and round worms parasitize man and cause many of his diseases. Ectoparasitic insects not only prey upon him but transmit in many cases the pathogenic organisms mentioned above. The battle against the disease-causing and disease-transmitting organisms is carried on by students of Medicine and of Public Health; and the biological sciences Bacteriology and Helminthology, dealing with microscopic organisms (mostly bacteria) and the parasitic worms, respectively, have assumed a very vital importance. It may come as a surprise to some readers to realize that antiseptic surgery dates only from 1870, and that the discoveries that tuberculosis was caused by bacteria, and that malaria was caused by protozoa, came in 1880. Not until 1900 was the life-cycle of the malaria organism and the relationship of the mosquito thereto worked out by specialists in Protozoölogy and Entomology. At about this same time the connection between yellow fever and the mosquito was demonstrated, but the causative organism was not discovered until nearly twenty years later. At the present time Medicine and Public Health have enlisted the services of specialists from every field of biological science in the battle against disease.

EUGENICS AND EUTHENICS

The development of the individual organism is, as we have seen in previous chapters, determined by two sets of factors, hereditary and environmental. And it is a matter of popular

knowledge that the physical characteristics of human beings are inherited in part and in part acquired.

Galton, one of the pioneers in the study of human inheritance, long ago formulated a famous law to the effect that one-half of the heritage is due to the parents, one-fourth to the grandparents, one-eighth to the great-grandparents, and so on. This law is applicable to mass populations and to such fluctuating characteristics as height, and the measurements of various parts of the body. More modern studies of heredity indicate that Galton's law holds for these fluctuating characteristics because they are affected by a large number of Mendelian factors, genes, and that the typical Mendelian behavior of any one gene is obscured by the others. There are also many instances of contrasting (allelomorphic) individual characteristics in man which follow the Mendelian laws with the same exactness as do those of other bisexual organisms.

A good example is shown by the inheritance of albinism, a condition in which pigment cells, chromatophores, are absent from eye and hair, so that individuals thus afflicted are pink-eyed and white-haired. This characteristic is due to a single recessive gene. Daltonian color-blindness, the inability to distinguish red from green, is due to a single recessive gene located in the sex-chromosome. The practical difficulties involved in tracing individual characteristics have prevented us from building up a very large body of information concerning the human genes. Probably fewer than fifty are known. Most of these concern marked physical disabilities, such as **haemophilia,** or bleeding caused by the absence of some of the proteins which cause blood clotting, and **brachydactylism,** or the absence of one of the finger joints. As the number of known genes is only about twice the haploid number of chromosomes (24), and since controlled experiments are hardly possible, little is known as to linkage, or the association of the genes in chromosome groups, in man.

Less is known concerning the inheritance of mental traits. The genealogical trees of the Jukes and the Kallikak families indicate the inheritance of undesirable traits manifested as feeble-mindedness, degeneracy, and crime, whereas on the other hand the Jonathan Edwards family has had an unusual number of descendants with superior mental ability. Studies of such case records have led to the establishment of a branch of Genetics known as Eugenics which is concerned with the improvement of

the human stock by selective mating. It is the belief of eugenists that, by restricting the right to bear children, undesirable genes may be bred out of the human stock, to the great advantage of coming generations. But so far as mental characteristics are concerned, too little is known of the method of inheritance, whereas the effects of the environment, particularly in conditioning reflexes, are obvious. Training and education as modifying factors can act, of course, only on the material transmitted through heredity, but where training and education can be controlled more exactly than heredity, it would appear judicious to walk slowly in enacting legislation until our knowledge of biological laws is more precise.

In contrast with Eugenics, another school of sociologists maintains that improvement in the race may be effected most rapidly by improving environmental conditions, a doctrine known as Euthenics. Extreme advocates of both schools have carried their arguments far beyond the limits which the biologist sets for himself. But since each appeals to Biology for supporting evidence, a knowledge of the laws of Genetics and of Ecology is essential for the inquiring student.

AGRICULTURE, AQUICULTURE, AND CONSERVATION

The relations between man and his environment are, of course, primarily ecological. His foods and the raw materials for his industries come, in large measure, from the bodies of other organisms, many of which he has domesticated to his use. The science of applied Biology known as Agriculture rests upon a knowledge of these domesticated plants and animals, their structure, functions, and development; of their genetic constitution and the environmental factors by which they are affected. This science includes the theory and practice of cultivating the soil, i.e., raising thereon animals (Animal Husbandry) or plants (Plant Husbandry).

Long a matter of transmitted tradition and often superstition, Agriculture now relies on the basic sciences of Biology and Chemistry for the theory on which current agricultural practice is based. Year by year man has wrested from nature additional territories on which to cultivate his crops and stocks, and some students of the subject tell us that the maximum limits are nearly reached. Further increases in yield must come from improved methods.

We know very little as to the origin of our domesticated plants and animals. But since plant and animal breeders have practiced hybridization and selection on a large scale and with reliance on genetic principles, great improvements in the quality and quantity of the products is observable. Only a small fraction of the quarter of a million species of plants are cultivated at all, and the number of intensively cultivated plants is very few. But year by year our federal Department of Agriculture sends trained botanists to every corner of the globe in the search for plants which may be of service when cultivated in the United States. Under the leadership of Thomas Edison, hundreds of so-called weeds are being studied in the attempt to find a domestic source of rubber. The proper cultivation of the soil is based on the study of plant and animal physiology, and the battle against organisms which cause disease in domestic plants and animals has given rise to the biological sciences of Plant Pathology and Animal Pathology.

Wherever man has made his habitation, cultivated the soil, or grazed his flocks, he has altered the balance of nature, and inaugurated far-reaching changes in the ecological equilibrium. Whether by felling the dominant trees, draining the swamps, or introducing alien species, the biotic conditions are disturbed. Immediately there are incursions of the swiftly moving, rapidly multiplying, and highly specialized insects, quick to prey on the new vegetation and animal types which man has introduced for his own purposes. Metcalf and Flint estimate that in 1924 the economic loss caused by insects in the United States alone was $1,590,044,500. Like the biblical "locust," incalculable myriads of insects threaten every crop from every conceivable angle; and broad acres of a single kind of plant stimulate the reproduction of the insect pests far beyond the normal rate.

The applied science of Economic Entomology devotes itself to the combating of these insect pests. By the development of sprays and dusting powders it is hoped that many insects may be exterminated at some stage in their life history. The establishment of national and state quarantines is designed to halt the migration of such pests as the gypsy-moth and the corn-borer. The introduction of other organisms which parasitize or prey upon the pest in question is a development of recent years. But the ancient maxim of setting a thief to catch a thief is not without its drawbacks. Without a careful study of the ecological re-

lationships of the form which it is desired to introduce, new dangers may be incurred. When the new species is acclimatized it may change its food habits and prey upon some beneficial or neutral insect instead of its former spoil.

In the United States within the memory of living men great areas have been reclaimed from nature. But more recently there has been a rapidly mounting demand for the conservation of natural resources. By this is meant the retention by the government, under so-called natural conditions, of certain areas where the mineral deposits or forests are of great economic importance. But the argument is not entirely an economic one, for these areas will soon be the only regions in which the ecologist can study " wild life " under natural conditions. The biologist is particularly concerned with the preservation of these areas and their utilization as refuges for species which otherwise might become extinct.

While the biological sciences find immediate application in Agriculture and the conservation of terrestrial resources, the newly developed science of Aquiculture or " water farming " is also of importance. The ocean supplies kelp from which fertilizer as well as certain chemicals of industrial importance are extracted, and newly developed methods of packing and transportation are increasing the use of sea-foods far into the interior. Only a few of the edible products of the sea are utilized as yet in this country, and the codfish, emblem of Massachusetts, still ranks as the most important single species used in America, although the salmon of the Pacific Coast is pressing it hard. Aside from the fishes already mentioned, the haddock, mackerel, halibut, swordfish, herring, and a score of others find their place in the national larder. Of the cartilage-fishes, the dogfish is marketed under a trade name, and the skate is esteemed a delicacy by a few. Of the crustaceans, the lobster, crab, and shrimp alone have commercial value. The molluscs offer a variety of fare of which only the surface has been touched in the utilization of the oyster, clams of three or four genera, the mussel, scallop, abalone of the Pacific, and among some of our foreign population, the squid and octopus. Biologists in the federal Bureau of Fisheries and elsewhere are being called upon to study the ecology and development of these forms and to offer practical suggestions as to their culture, to the end that the ocean may some day be farmed scientifically rather than hunted sporadically. Already great advances have been made in oyster culture.

Inland, the rivers supply a quota of the nation's food through the medium of the commercial fishes such as the carp, buffalo, and catfish, marketed in great numbers from the Mississippi and its tributary waters. Of recent years the inland fisheries have felt the malignant effects of pollution through sewage and the wastes of factories. The reports of the Illinois State Natural History Survey show how a stream has been polluted for hundreds of miles by the wastes of a great city. Incidentally, by a careful study of the plants and animals to be found in polluted waters, it has been discovered that different species are able to live under varying degrees of pollution, so that it is possible to utilize the various groups as biological indices of pollution. Studies of the food habits and developmental histories of the important commercial and game fishes are of great importance to state departments of conservation.

IN CONCLUSION

In concluding this introduction to biological science it may not be amiss to recall to the reader's attention that he set out to study life, something manifested only in plants and animals. In doing this he found himself from time to time using the methods of other sciences. In order to describe the structure and functions of organisms, and to analyze these in terms of the biological unit, the cell, the biologist must become a biochemist and a biophysicist. When he studies behavior, particularly in its more complex manifestations, he finds himself trespassing on the psychologist's preserves. The geneticist must, perforce, turn mathematician, and the ecologist wears the garments of the geographer, climatologist, and oceanographer. The student of evolution must learn to read the rocks with the geologist.

All this is a commonplace of modern science. So tenuous are the boundaries between the sciences, that the investigator, like all adventurers, sometimes emerges from the wilderness into his neighbor's estate. The trail of Biology is often tortuous, but the goal is always the understanding of life.

In our day the guiding hypothesis of many biologists is the physico-chemical conception of life, according to which the principal distinction between living and inanimate objects is the greater degree of complexity distinguishing the former. Further research may show us that this hypothesis is untenable. In the meantime it is pointing the way to the discovery of new facts

and the formulation of new theories to be tested by experiments and weighed against the findings in other fields. The facts often have a very practical application in human life; the theories are bound to influence contemporary thought. An understanding of modern civilization demands some knowledge of modern Biology.

APPENDIX I

GLOSSARY

In this glossary are included all technical terms used in the text, with the exception of taxonomic names which will be found in the tables of classification. The syllable most heavily accented is indicated. The plural is usually formed by adding "s" unless otherwise indicated.

A

abdo'men. The part of the body posterior to the thorax.
abduc'tor. A muscle which moves a bone away from the midline of the body.
abiogen'esis. The theory that living organisms may arise from inanimate matter.
abo'ral. The surface of the body away from the mouth.
absorp'tion. Passage of material through the plasma membrane into the cell.
accre'tion. Growth by the addition of parts externally.
adduc'tor. The muscle which moves a bone toward the middle of the body.
ad'ipose. Fatty.
adjus'tor. A neurone entirely contained in the central nervous system.
adre'nal. An internally secreting gland located on or near the kidney.
ag'riculture. The science of cultivating the ground.
aleu'rone. A layer in the grain of wheat (Fig. 53).
alle'lomorph. One of a pair of contrasting genes or the characters resulting from their presence.
ami'no acid. An organic acid containing NH_2 and COOH radicles; obtained by breaking down proteins.
amito'sis. Method of cell division in which chromosomes are not formed.
amphimix'is. Term applied to the bringing together of chromatin (or genes) from two parental sources.
amplex'us. The sexual embrace of Amphibia.
anab'olism. The chemical reactions which taken together result in a growth of protoplasm.
anal'ogy. A resemblance in form due to a similarity of function. Contrast homology.
an'aphase. A stage in mitosis in which the daughter chromosomes draw apart.
anisog'amy. The process of fusion between unlike gametes.
an'ther. The microspore (pollen) forming organ (of the stamen) of flowering plants *See* microsporangium.
antherid'ium (pl. antheridia). The microgamete (or sperm) forming organ in all non-flowering plants.
anthropol'ogy. The science which has to deal with the human body, and in a larger sense the study of primitive man.
an'timere. One of a number of corresponding parts in a radially symmetrical animal.
antip'odal. At the end away from the pole.
a'nus. The posterior opening of the digestive tube.
aor'ta. The principal axial artery of the body.
appendic'ular. Having to do with the appendages of the body.
a'queous hu'mor. The liquid found in the anterior portion of the eyeball.
a'quiculture. Science of cultivating the waters.

archaeol'ogy. The science which has to deal with the artifacts of primitive human races, and in a larger sense the study of their culture.
archego'nium (pl. archegonia). The organ in which the egg is formed in non-flowering plants.
ar'tery. A blood-vessel carrying blood away from the heart.
articula'tion. A joint or juncture between parts of the skeleton.
as'cospore. A type of spore formed by the Ascomycetes.
asex'ual. A form of group production in which male and female germ cells are not formed and syngamy does not occur.
assimila'tion. The process by means of which absorbed material is added to protoplasm.
associa'tion. A developing community.
asso'cies. A small community differing from the surrounding association because of local (edaphic) factors.
at'las. The vertebra articulating directly with the skull.
a'trium (pl. atria). Chamber of the heart which receives the blood from the veins. *See* auricle.
au'ditory. Having to do with the sense of hearing.
au'ricle. Chamber of the heart which receives the blood from the veins. *See* atrium.
autecol'ogy. That branch of ecology which is concerned with the factors affecting a single species. Contrast synecology.
autocat'alyst. A catalytic agent which increases its own substance.
autono'mic. Semi-independent. That part of the nervous system which innervates the smooth muscles of vertebrates.
autophyt'ic. Type of nutrition found in green plants which manufacture their food by photosynthesis.
awn. The beard of the wheat grain.
ax'ial. Along the main axis of the body.
ax'il. The angle between the upper side of a branch or leaf and the stem from which it arises.
ax'is. A line passing through the body around which parts are symmetrically arranged; (2) the second neck vertebra.
ax'on. Process of a nerve cell; nerve fiber.

B

bacil'lus (pl. bacilli). Type of bacteria characterized by its rod-like shape.
bacteriol'ogy. The science dealing with the study of bacteria.
basid'ium (pl. basidia). A club-shaped hypha from which arise the asexual spores in the Basidiomycetes.
ben'thos. The fauna and flora found below the photic zone.
bile. The fluid secreted by the liver.
bino'mial nomencla'ture. The Linnaean system of identifying organisms by means of their generic and specific names.
biogen'esis. The theory that organisms are formed only by reproduction of other organisms. Contrast abiogenesis.
biol'ogy. The science which has to do with life.
bipenna'ria (pl. bipennariae). A form of larva peculiar to the starfish and other Asteroidea.
blad'der. A sac-like organ for temporary storage of a fluid.
blas'tocoele. The cavity of the blastula.
blas'tomere. One of the cells formed by cleavage prior to the formation of the germ layers.
blas'topore. An opening by means of which the cavity of the gastrula connects with the exterior.
blas'tula. The early embryo prior to the segregation of the germ layers.
blas'tostyle. A hydranth from which are budded medusae (Fig. 101).
bot'any. The science which deals with plants.
bud. (1) Protuberance from which develops a new organism; (2) a protuberance in the axil of a stem or branch from which new stems or leaves develop.

C

cam'bium. Growing tissue in the dicotyledons between the xylem and phloem of the vascular bundles.
cap'illary. A blood vessel of small caliber often connecting arteries and veins.
car'apace. An exoskeletal covering of the thorax.
carbohy'drate. A compound of carbon, hydrogen and oxygen with twice as many atoms of hydrogen as oxygen.
car'dinal. A large vein found in the embryos of all vertebrates and the adults of the anamniotes.
car'otin. A yellow pigment found in plastids.
car'pal. A megasporophyll found in the flowering plants, several of which may fuse to form the pistil although this sometimes arises from a single carpal.
car'tilage. Gristle.
castra'tion. The removal of the ovaries or testes.
catab'olism. The process of breaking down protoplasm.
catal'ysis. The act of accelerating a chemical reaction by a substance (the catalyst) which itself remains unaltered.
ca'val. The veins which return the blood to the heart in higher vertebrates.
cell. A mass of protoplasm containing a nucleus and surrounded by a membrane; the structural unit of organisms.
cel'lulose. A carbohydrate usually found in the wall of plant cells.
cen'trosome. A minute self-perpetuating body found in cytoplasm, usually concerned in mitosis.
cerca'ria (pl. cercariae). A larval form of the liver fluke.
cerebel'lum. A structure developed from the roof of the vertebrate netencephalon.
cere'brum. A structure developed from the roof of the vertebrate telencephalon; containing the center association.
chap'arral. The vegetation area intermediate between desert and forest in warm, dry regions.
chemosyn'thesis. A method of nutrition found in some unicellular plants (bacteria) in which the energy for building up foodstuffs is obtained by the breaking down of other substances.
chi'tin. A horny substance found in the exoskeleton of arthropods.
chloren'chyma. Parenchymatous tissue containing chloroplasts.
chlo'rophyll. Green coloring matter found in chloroplasts concerned in photosynthesis.
chlo'roplast. Self-reproducing cytoplasmic body containing chlorophyll.
chon'driosome. Minute self-reproducing cytoplasmic bodies which stain with Jenus B in living tissue.
cho'roid. A thin vascular layer, e.g., choroid layer of the eyeball.
chro'matin. A substance in the nucleus which stains deeply with basic dyes.
chromid'ium (pl. chromidia). A particle of chromatin not confined in a nuclear membrane.
chro'moplast. A red or brown plastid.
chro'mosome. A body of chromatin observable in mitotic cell division characterized by its individuality in self-reproduction.
cil'ium (pl. cilia). A hair-like motile organelle characteristic of certain cells and tissues.
circula'tion. The function of distributing materials throughout the body.
class. The principal subdivision of a phylum or sub-kingdom.
cleav'age. Process by which the egg is divided into blastomeres.
cli'max. An association in equilibrium with its climatic factors.
clitel'lum (pl. clitella). A distended region in earthworms rich in glands.
cloa'ca (pl. cloacae). The posterior region of the enteron into which urinary and genital ducts open.
coc'cus. A spherical form of bacteria.
coe'lom. A cavity of the body between the digestive tube and the body wall.
coenogenet'ic. A character appearing in embryology which is not considered the recapitulation of an ancestral character. Contrast palingenetic.
coleop'tile. Embryonic shoot in the development of a sea plant.
coleorhi'za. Embryonic root in the development of a sea plant.

col'ony. An aggregation of cellular individuals arising from the same parent which remain in a state of physical union or close coöperation.
columel'la. A bone in the middle ear.
commen'sal. An organism living in intimate association with one of another species, without advantage or disadvantage to either.
conjuga'tion. The temporary union between two cells with an interchange of nuclear material.
cor'nea. The transparent region of the eyeball.
cor'puscle. A minute body such as the blood cell.
cor'tex. An outer layer; (1) the region between the epidermis and the endodermis in the root and stem of vascular plants; (2) roof of the vertebrate telencephalon; (3) the outer layer of the vertebrate kidney or adrenal gland, etc.
cotyle'don. The seed leaf of the sporophyte embryo in spermatophytes.
crenula'tion. Shrinking of an animal cell in a hypertonic solution.
culm. The stem of grasses such as wheat.
cuta'neous. Having to do with the skin.
cyst. A wall or envelope formed about an organism, protective in nature.
cysticer'cus (pl. cysticerci). A larval stage of the tapeworm.
cytol'ogy. The study of the cell.
cytol'ysis. Bursting of the cell wall in a hypotonic solution.
cy'toplasm. Protoplasm of the cell exclusive of the nucleus.

D

dedifferentia'tion. Process in which specialized cells return to a more generalized condition. Contrast differentiation.
dehydra'tion. A chemical reaction in which hydrogen ions are removed from one molecule and hydroxyl ions from another to unite and form water.
den'drite. Protoplasmic process of a neurone.
depres'sor. A muscle whose contractions pull a bone ventrally from its normal position.
der'mis. Lower layer of the skin.
di'aphragm. The muscular partition separating the abdominal and pleural cavities in mammals.
dic'tyosome. Self-reproducing cytoplasmic body often uniting with others to form a Golgi network.
dienceph'alon. Part of the vertebrate brain lying between the telencephalon and mesencephalon.
differentia'tion. Process of transformation from less complex to more complex organization. Contrast dedifferentiation.
diffu'sion. Movement of particles in solution towards a state of equilibrium.
digam'ety. Formation of two different classes of gametes in one sex; e.g., in most vertebrates the male gives rise to two classes of spermatozoa, male-producing and female-producing.
diges'tion. Function of breaking down chemical compounds in food to simpler compounds which can be absorbed into the body.
dioe'cious. In animals a species in which the sexes are separate; in plants a species in which one sporophyte has staminate (male) flowers, while another has pistilate (female). Contrast monoecious.
dip'loid. With double number of chromosomes found in the fertilized egg and in all cells arising therefrom prior to reduction. Contrast haploid.
dissimila'tion. Sum total of chemical reactions by means of which the amount of protoplasm is reduced.
dis'tal. That end of a part of organ farthest from the midline of the body.
dom'inant. In genetics, the one of a pair of allelomorphic characters which produces a visible effect when both are present. Contrast recessive. In ecology, that species of community which has the greatest biotic effect on the character of the community.
dor'sal. The back or upper side. Contrast ventral.
dy'ad. A chromosome of two parts.

E

ecol'ogy. Study of the organism within a community.
ec'toderm. Outermost germ layer.
edaph'ic. Local conditions, mainly with reference to water and soil.
effec'tor. That part of the organism which responds to stimulation.
em'bryo. Stage in the development of the organism.
embryol'ogy. Study of the development of organisms.
en'docrine. Product of a ductless or internally secreting gland.
endocrinol'ogy. Study of endocrines.
en'doderm. The innermost germ layer.
endoder'mis. Layer of cells surrounding the vascular cylinder in the higher plants.
en'dolymph. A fluid found in the membraneous labyrinth of the inner ear.
endomix'is. Process of nuclear reorganization without syngamy: a variety of parthenogenesis in protozoa.
en'dosperm. A tissue with reserve food material, found in the seed.
endother'mic. A chemical reaction in which kinetic energy is converted into potential energy.
en'teron. The digestive cavity.
entomol'ogy. Study of insects.
enu'cleate. Without a nucleus.
envi'ronment. The sum of all factors external to an organism by which its life is affected.
en'zyme. Catalytic agent formed by protoplasm.
epider'mis. External layer of tissue in both plants and animals.
epigen'esis. The theory that the organism develops progressively from a relatively simple to a relatively complex organization. Contrast preformation.
eugen'ics. School of sociology which believes in improving the human race through the control of hereditary factors. Contrast euthenics.
euthen'ics. School of sociology which believes in improving the human race through the control of environmental factors. Contrast eugenics.
evolu'tion. Theory that new species have arisen from the modification of other species.
excita'tion. A state of metabolic activity aroused by stimulation which may be transmitted from cell to cell.
excon'jugant. A protozoan which has just separated from its mate following conjugation.
excre'tion. Function of disposing of a waste product formed in dissimilation.
ex'ine. The outer spore coat.
exother'mic. Chemical reaction in which potential energy is converted into kinetic energy.
exten'sor. A muscle whose contraction results in the extension of the angle between two articulated bones.

F

fam'ily. The principal subdivision of a class in classification.
fe'mur. The thigh bone.
fenes'tra (pl. fenestrae). An opening in a bone.
fertiliza'tion. Syngamy between an egg and a spermatozoan.
fib'ula (pl. fibulae). One of the two shin bones.
fibula're. One of the metatarsal bones articulating with the fibula.
fil'ament. Stalk of a stamen which supports the anther.
flagel'lum (pl. flagella). A whip-like motile process of certain cells.
flex'or. A muscle whose contraction diminishes the angle between two articulating bones.
fore'gut. Anterior region of the enteron in vertebrate embryos.
formal'dehyde. Poisonous chemical substance formed in one of the steps of photosynthesis.
forma'tion. The plants and animals existing under similar climatic conditions in a given geographical area.
fos'sil. Petrified remains of an organism.
frond. The sporophyll of ferns and their allies.

G

gametan'gium (pl. gametangia). The organ of plants in which the gametes are formed. *See* antheridium and archegonium.
gam'ete. A mature germ cell.
gam'etophore. Shoot-like branches of the moss gametophyte on which the gametangia are found.
gam'etophyte. The sexual generation of multicellular plants by which the gametes are produced.
gan'glion. An aggregate of nerve cells outside the neural tube in vertebrates.
gastrocne'mius. A muscle of the vertebrate leg. See Fig. 17.
gas'trocoele. A cavity of the gastrula.
gas'trula (pl. gastrulae). An embryo in which the ectoderm and endoderm are segregated.
gemma'tion. An asexual form of reproduction; budding.
gene. The unit of modern genetics: an invisible self-reproducing element found in linear aggregation in the chromosomes.
genet'ics. The study of heredity.
gen'otype. One of the possible classes differing in genetic constitution arising from hybridization. Contrast phenotype.
ge'nus (pl. genera). In classification the principal subdivision of a family.
ger'minal. Congenital; transmitted in heredity. Contrast somatic.
germina'tion. The beginning of growth from spore or seed.
germ layers. The first differentiated tissues appearing in the embryo. *See* ectoderm, endoderm, mesoderm.
gland. A secretory cell or group of cells.
glochid'ium (pl. glochidia). A larval stage found in the development of molluscs.
glomer'ulus (pl. glomeruli). A network of capillaries found in close association with a kidney tubule.
glot'tis (pl. glottides). Opening into the trachea.
glu'cose. The simplest carbohydrate; sugar.
glume. A modified leaf inclosing the spikelet of a grass flower, as of wheat.
gly'cogen. A complex carbohydrate somewhat similar to starch, found in animals.
gon'ad. A gland in which the gametes develop in animals. *See* ovary, testis.
grad'ient. A direction in which a variable increases or decreases, e.g., diffusion gradient.
gutta'tion. The exudation of water from leaves in periods of high temperature and little wind current.
gynan'dromorph. An individual in which both male and female characteristics are evident.

H

haem'ocoele. The large cavity containing blood found in the arthropods.
haemoglo'bin. A chemical compound found in red blood corpuscles to which atoms of oxygen are easily added and from which they are given off.
hap'loid. The number of chromosomes found in the gametes. Contrast diploid.
helminthol'ogy. The study of worms, particularly parasitic forms.
hepat'ic. Having do to with the liver.
hermaph'rodite. An individual which produces both male and female gametes.
heteros'porous. Plants which give rise to both microspores and megaspores in the same individual. Contrast homosporous.
heterotyp'ic. The first maturation division, so called because it differs from the ordinary mitosis. Contrast homoeotypic.
heterozy'gous. Producing two types of gametes with respect to the member of a pair of allelomorphic genes which it contains. Contrast homozygous.
hind'gut. The posterior portion of the enteron in a vertebrate embryo.
histol'ogy. The study of tissues.
holophyt'ic. A type of nutrition characteristic of the green plants. *See* autophytic.
holozo'ic. A type of nutrition characteristic of animals, which ingest solid particles of food. Contrast holophytic.

homoeotyp'ic. The second maturation division, which resembles a normal mitotic division. Contrast heterotypic.
homol'ogy. A resemblance in form or structure regardless of function and supposedly due to descent from a common ancester. Contrast analogy.
homos'porous. Plants in which the sporophyte produces either megaspores or microspores. Contrast heterosporous.
homozy'gous. An individual producing gametes all of which have the same member of a pair of allelomorphic genes. Contrast heterozygous.
hor'mone. An internal secretion. *See* endocrine.
hy'brid. The heterozygous offspring of parents which differ in one or more pair of allelomorphic characters.
hy'dranth. A *Hydra*-like individual of a coelenterate colony.
hydrol'ysis. A type of chemical reaction in which a compound is broken down by the addition of water.
hyperton'ic. A solution greater in molecular concentration than the one with which it is compared. Contrast hypotonic.
hypoton'ic. A solution of lesser molecular concentration than the one with which it is compared. Contrast hypertonic.
hy'pha (pl. hyphae). Filamentary structures characteristic of the fungi.

I

inflores'cence. A compound flower.
in'fluent. An organism which while not dominating exerts an influence on the character of a community by its presence.
inhibi'tion. Restraining the function of an organ or part.
inser'tion. That end of a muscle farthest from the point of leverage. Contrast origin.
in'stinct. A type of animal behavior performed without previous practice.
in'ternode. Region of the stem between two nodes.
in'tersex. Individuals with irregular sexual characteristics due to aberrations of the sex-chromosomes.
intes'tine. Region of the enteron posterior to the stomach.
in'tine. The inner layer of the spore wall.
intussuscep'tion. The act of adding new material throughout the mass by the object added to. Contrast accretion.
i'ris. A membrane partially dividing the eyeball into anterior and posterior chambers. *See* Fig. 21.
irritabil'ity. Property of responding to stimulation.
iso'gamy. The formation of gametes which are morphologically similar. Contrast anisogamy.
isoton'ic. A solution with similar molecular concentration to that of the one with which it is compared.

K

kar'yoplasm. Protoplasm within the nuclear wall.
kar'yosome. A body within the nucleus having the same staining reaction as chromatin.

L

lar'va (pl. larvae). Stage of development exhibiting all the functions except that of reproduction and differing in form from the adult, e.g., tadpole.
lem'ma. One of a pair of bracts internal to the glume in the grass flower.
lens. The biconvex transparent body in the eyeball which focuses the light rays upon the retina.
leu'coplast. A colorless plastid.
leva'tor. A muscle whose contractions lift the bone to which it is attached.
lig'ule. A scale-like structure where a sheath of a wheat leaf opens up to form the blade.

link'age. The inheritance of two or more characters in association with each other owing to the location of their respective genes in the same chromosome.
lip'in. An organic compound containing carbon, oxygen, and hydrogen, generally fatty in nature.
lit'toral. Pertaining to the shore.
lod'icule. A scale-like structure in the wheat flower enclosing the stamens and pistil.
lymph. Blood plasma and white blood corpuscles which have passed through the walls of the capillaries.

M

macronu'cleus (pl. macronuclei). The larger of the two kinds of nuclei found in ciliates. *See* meganucleus.
mar'row. Tissue found in the cavity of bones.
matura'tion. The act of becoming mature; the divisions by means of which chromosomes are reduced from the diploid to the haploid number.
medul'la (pl. medullae). (1) The internal tissue of organs such as the kidney or adrenal. (Contrast cortex.) (2) Part of the brain stem. *See* myelencephalon.
medu'sa (pl. medusae). The free-swimming coelenterate individual. Contrast hydranth.
megagam'ete. The larger of a pair of gametes formed in anisogamous species: the egg.
megagametan'gium (pl. megagametangia). *See* archegonium.
megagam'etophyte. An egg-producing gametophyte.
meganu'cleus (pl. meganuclei). The larger of the two types of nuclei found in ciliates. *See* macronucleus. Contrast micronucleus.
megasporan'gium (pl. megasporangia). The organ in which megaspores are formed.
meg'aspore. The large spore from which develops a female gametophyte. Contrast microspore.
megaspo'rophyll. A spore-bearing leaf of a flower from which megaspores are produced. *See* carpel.
mer'istem. One of the primary tissues in the developing plant.
mesenceph'alon. Middle portion of the vertebrate brain in the roof of which the optic lobes are found.
mes'oderm. The middle germ layer.
mesogloe'a. A supporting layer found between the ectoderm and the endoderm of coelenterates, non-cellular in nature.
mesoneph'ros. Type of kidney found in adult fish and amphibia and embryos of higher vertebrates.
mes'ophyll. The middle layer of the leaf.
metab'olism. The property of undergoing chemical change characteristic of protoplasm.
met'amere. One of a number of serially analogous parts.
metamor'phosis (pl. metamorphoses). A change in structure such as the transformation of the tadpole into the frog or the spermatid into the spermatozoan.
met'aphase. That stage in mitosis in which the chromsomes form a plate across the equator of the dividing cell.
met'aphyte. A multicellular plant.
metaplasm. Bodies in the cell which are products of the protoplasm.
metatar'sal. Bones of the foot between the ankle and toes.
met'azoon (pl. metazoa). A multicellular animal.
metenceph'alon. Portion of the brain between the mesencephalon and myelencephalon, from the roof of which arises the cerebellum.
microgam'ete. Smaller member of a pair of anisogamous gametes: the sperm.
microgam'etophyte. Sexual plant producing only microgametes.
micronu'cleus (pl. micronuclei). The smaller nucleus of ciliates. Contrast meganucleus.
microsporan'gium (pl. microsporangia). Organ of sporophyte which produces microspores. Contrast megasporangium.
micro'spore. The small spore from which arises a microgametophyte. Contrast megaspore.

microspo'rophyll. Spore-forming leaf which produces only microspores: the stamen of a flowering plant. Contrast megasporophyll.
mid'gut. The middle portion of the enteron of the vertebrate embryo.
milt. The sperm-containing fluid emitted by the male.
miracid'ium (pl. miracidia). One of the larval stages of the liver fluke.
mito'sis (pl. mitoses). Form of cell division in which chromosomes appears. Contrast amitosis.
monoe'cious. In zoölogy, an individual producing both male and female gametes; in botany, a plant which produces both eggs and sperm but in different flowers (stamenate or pistillate). Contrast dioecious.
morphol'ogy. Division of biology concerned primarily with form or structure.
mo'tor. Type of neurone conveying a nervous impulse from the central nervous system to an effector.
muco'sa. The inner, glandular layer of the digestive tube.
myce'lium. A mass of hyphae found in fungi.
myelenceph'alon. The posterior portion of the vertebrate brain connecting with the spinal cord; the medulla oblongata.
my'elin. The sheath surrounding the axon of some neurones.
myofi'bril. A contractile fiber such as is found in muscle cells.
my'sis. A larval stage in some crustacea; e.g., the lobster.

N

nat'ural his'tory. A term formerly used to include the study of plants, animals and minerals, contrasted with civil history.
nau'plius. A larval stage of some crustacea.
nec'tary. The nectar-producing gland of flowers.
neolith'ic. Having do do with the age of polished stone implements.
neph'ric. Having to do with the kidney.
neph'rostome. A ciliated opening connecting the nephric tubule and the coelom.
neph'rotome. A metameric division of the mesoderm in vertebrate embryos from which the kidneys arise.
neu'ral. Having to do with the nervous system.
neurenter'ic. Name applied to the canal connecting the neural tube with the enteron in some early vertebrate embryos. *See* Fig. 30.
neu'rone. A nerve cell.
node. A growing point.
non-disjunc'tion. Failure of daughter chromosomes to separate in maturation.
no'tochord. An axial supporting rod characteristic of all chordates at some stage of development.
nucel'lus (pl. nucelli). A layer of the ovary which represents the megasporangium of spermatophytes.
nucle'olus (pl. nucleoli). Small body in the nucleus: karyosome or plasmasome.
nu'cleus (pl. nuclei). A characteristic body containing chromatin, found in all cells except those in which the chromatin is scattered throughout the cytoplasm.
nutri'tion. The phenomena concerned with food: the study of food.

O

oesoph'agus. Portion of the digestive tract anterior to the stomach.
olfac'tory. Having to do with the sense of smell.
ontog'eny. The life history of the individual. Contrast phylogeny.
o'öcyte. In animals the female germ cell prior to the maturation divisions: an immature egg.
oögo'nium (pl. oögonia). Germ cell found in the ovary prior to its growth into an oöcyte. (2) In plants, that cell of a colony which will become a macrogamete.
oper'culum (pl. opercula). A covering, e.g., structure covering the internal gills of the tadpole.
op'tic. Having to do with the sense of sight.
o'ral. That side or surface on which the mouth opening is found. Contrast aboral.

or'der. In classification, the principal subdivision of a class.
or'gan. A mass of tissue or tissues specialized for a specific function.
organelle'. The portion of a single cell specialized for a specific function.
or'ganism. A plant or animal as distinguished from an inanimate object.
organiza'tor. A region or structure in embryology the localization of which acts as a stimulus to further differentiation.
organother'apy. The use of endocrine organs and their products in medicine.
or'igin. That end of a muscle attached to the relatively immovable part of the skeleton. Contrast insertion.
ornithol'ogy. The study of birds.
os'culum (pl. oscula). The excurrent opening of the sponge colony.
osmo'sis. Passage of water through a semi-permeable membrane. (*This word is used in so many senses that no generally acceptable short definition can be given.*)
o'vary. The organ in which macrogametes or eggs are formed or developed.
o'viduct. Duct through which the eggs are conveyed to the exterior.
o'vule. The seed-forming organ of the flower.
o'vum. Megagamete: egg.

P

palaeobot'any. Study of extinct species of plants.
palaeolith'ic. Pertaining to the age of unpolished stone implements.
palaeontol'ogy. Study of extinct plants and animals.
palaeozoöl'ogy. Study of extinct animals.
pa'lea (pl. paleae). Bract of a wheat flower opposite a lemma.
palingenet'ic. Embryonic characteristics supposedly reminiscent of ancestral characteristics. Contrast coenogenetic.
pan'creas. A digestive gland of the vertebrates.
parathy'reoid. Endocrine glands of vertebrates found near the thyreoid gland.
paren'chyma. Connective tissue.
parthenogen'esis. Type of sexual reproduction in which the egg develops without syngamy.
pathogen'ic. Causing disease.
pathol'ogy. Study of disease.
pedun'cle. The stem of the flower.
pelag'ic. Having to do with the surface waters of the ocean.
pel'vis. Bones of the hip in vertebrates.
pericar'dium (pl. pericardia). Tissue lining the cavity which contains the heart.
per'icarp. An outer seed coat.
perichon'drium. Tissue surrounding cartilage.
per'icycle. A layer of cells surrounding the vascular cylinder in seed plants.
per'ilymph. Fluid surrounding the membraneous labyrinth of the ear.
perios'teum. Tissue surrounding bone.
pet'als. Leaves of the flower immediately surrounding the stamens and pistils.
pha'lanx. One of the joints of the fingers or toes.
phar'ynx. Region of the digestive tube between the mouth and the oesophagus in chordates.
phe'notype. One of the different classes which can be distinguished from each other arising from hybridization. Contrast genotype.
phloem. A vascular tissue of the higher plants through which the sap descends; contrast xylem.
photosyn'thesis. Process by which the green plant builds up organic compounds from carbon dioxide and water using energy derived from sunlight.
phylog'eny. The life history of a species or any other group of classification. Contrast ontogeny.
phy'lum (pl. phyla). The main subdivision of the plant or animal kingdom: subkingdom.
physiol'ogy. The study of plants and animals, particularly with reference to their functions.
pin'eal. Having to do with an outgrowth from the roof of the diencephalon, once a median eye, now an endocrine gland.
pis'til. An organ of the flower composed of fused carpels, megasporophylls.

pitu'itary. Having to do with an endocrine organ formed partially from the midbrain and partly from an outgrowth of the embryonic mouth.
placen'ta (pl. placentae). An organ for the nourishment of the developing embryo, such as the mammalian placenta or the placenta of the ovary in seed plants.
plac'odes. A plate-like region in the ectoderm from which arise sensory or nervous elements of the vertebrate embryo.
plank'ton. Floating organisms which form surface communities in the sea or fresh water.
plan'ula (pl. planulae). A creeping larva found among coelenterates.
plas'ma. The liquid of the blood.
plas'ma mem'brane. Protoplasm which forms the surface layer of the cell.
plas'masome. An intranuclear body which does not contain chromatin. Contrast karyosome.
plasmo'dium (pl. plasmodia). An irregular aggregate of cells without distinct cell boundaries.
plasmol'ysis. Collapse of the cell wall in a hypertonic solution.
plas'tid. Self-reproducing cytoplasmic bodies often concerned with reproduction, e.g., chloroplast.
pleu'ral. Having to do with the cavity in which the lungs are found.
plex'us. A network of nerve fibers.
plu'mule. The primordium of the shoot of the embryo in higher plants.
pole. A point of direction of the egg often associated with the region of greatest activity.
pol'len. Microspores of spermatophytes.
po'locyte. Miniature cells formed in the maturation of the egg; polar bodies.
pol'yploid. Having a multiple of the haploid number of chromosomes, e.g., triploid, tetraploid, etc.
predom'inant. A species having great influence as a biotic factor in a community.
prehal'lux. An extra digit found in the foot of the frog to the side of the great toe.
preforma'tion. The theory that development is the growth of an individual already delineated from the egg or sperm. Contrast epigenesis.
primor'dium (pl. primordia). The first recognizable indication of the appearance of a new structure in development.
procam'bium. The primary meristems of the developing plant.
proctodae'um (pl. proctodaea). An inpushing of ectoderm to form the cloacal region of vertebrates.
proglot'tis (pl. proglottides). One of the segments of the tapeworm.
proneph'ros (pl. pronephroi). An embryonic type of kidney found in all vertebrates.
pronu'cleus (pl. pronuclei). Nucleus of the egg or sperm after fertilization prior to the first cleavage division.
pro'phase. First stage of mitosis in which the chromosomes appear and split longitudinally preparatory to division.
propriocep'tor. Sensory element which receives stimuli originating within the body.
pro'tein. Class of organic chemical compounds containing nitrogen, built up of amino acids.
prothal'lus. The gametophyte of ferns, so called because of its thallus-like structure.
protis'ta. Name applied to all unicellular organisms.
pro'toderm. One of the primary meristems of the plant which gives rise to the epidermis.
protone'ma (pl. protonemata). The gametophyte of the moss from which arise the gametophores which are usually taken for the moss plant.
pro'tophyte. A unicellular plant.
pro'toplasm. The living contents of the cell.
protozoöl'ogy. The science of unicellular animals.
pro'tozoön (pl. protozoa). A unicellular animal.
prox'imal. That part of the structure nearest the midline of the organism. Contrast distal.
pseudopo'dium (pl. pseudopodia). Irregular protoplasmic processes changeable in shape and used in locomotion, ingestion, etc.
pul'monary. Having to do with the lungs.
pu'pa (pl. pupae). Stage in the development of some insects in which the larva undergoes a metamorphosis into the adult.
pu'pil. Aperture in the iris of the eye.

R

rachil'la. The stem of a spikelet in the compound grass flower.
ra'chis (pl. rachides). The stem of the spike of the grass flower.
recapitula'tion. The theory that the embryo in its development repeats the history of the race.
recep'tacle. The base of the flower.
recep'tor. The structure by means of which a particular kind of stimulus is received.
reces'sive. One of a pair of allelomorphic characters which produces no visible effect when its dominant mate is present. Contrast dominant.
re'dia (pl. rediae). A larval stage of the liver fluke.
reduc'tion. (1) Process of reducing the number of chromosomes from the diploid to the haploid number in which synaptic mates are separated. (2) A chemical process in which oxygen is given off. Contrast oxidation.
re'flex. A unit of a pattern of synaptic behavior; mechanism involves at least one sensory and one motor neurone.
refrac'tory. A period following the transmission of an impulse along a nerve fiber during which another impulse cannot be transmitted.
regenera'tion. Process of reproducing parts of an organism. Compare asexual reproduction.
re'nal. Having to do with the kidney.
reproduc'tion. The power of organisms or parts of organisms to reproduce themselves.
respira'tion. Exchange of carbon dioxide and oxygen by protoplasm.
ret'ina. Sensory layer of the eyeball.
rhi'zoid. Root-like structure found in bryophytes and the gametophytes of ferns.
rhi'zome. The underground stem of fern sporophytes.
rhi'zophore. The aerial stem of *Selaginella.*
rota'tor. The muscle whose contractions cause a bone to rotate in a ball and socket joint.

S

sap'rophyte. A type of nutrition in which organic compounds are absorbed. Contrast holozoic and holophytic.
sar'code. The name applied to the protoplasm of the protozoön, and perpetuated in the class-name Sarcodina.
sciat'ic. A large nerve leading to the hind leg of vertebrates.
sci'on. A bud or twig grafted onto the body of another tree.
scle'ra. A tough connective tissue layer surrounding the eyeball.
sco'lex. The head or attaching portion of the tapeworm.
secre'tin. The endocrine formed in the mucosa and carried in the blood stream to the pancreas, thereby stimulating the production of pancreatin.
secre'tion. The act of passing from the cell through a semi-permeable plasmic membrane. Contrast absorption.
seed. The embryo of a sporophyte together with its reserve food and protective membranes.
senes'cence. Period in the life history following the attainment of sexual maturity during which the vital activities are lessened; old age.
sen'sory. Having to do with the reception of stimuli or the transmission of nervous impulses from sense organ to central nervous system. Contrast motor.
se'pal. One of the external whorl of leaves in a flower.
sex'ual. Having to do with sex: that type of reproduction in which eggs or sperm are formed.
shoot. Part of the seed plant which grows upward; stem and leaves. Contrast root.
skel'etal. Pertaining to the skeleton.
so'ma (pl. somata). The body as opposed to the germ cells.
somat'ic. Having to do with the soma. Contrast germinal.
so'mite. A metameric division of the body.
spawn. Sexual product of the female containing eggs. Contrast milt.

spe'cies (pl. species). Principal subdivision of a genus; an aggregate of individuals with similarities which would lead to the belief in a common ancestry. (*Note: No completely satisfactory definition of a species has yet been written.*)
sperm. Male or microgamete; spermatozoön.
sper'matid. Male germ cells of animals after maturation but before metamorphosis.
sper'matocyte. Male germ cells of animals prior to maturation divisions.
spermatogo'nium (pl. spermatogonia). Male germ cells of animals prior to their growth into spermatocytes.
spermatozo'ön (pl. spermatozoa). *See* sperm.
sphinc'ter. Circular muscle.
spike. A cluster of spikelets.
spike'let. The grass flower.
spin'dle. A bundle of fibers tapering towards each end along which the chromosomes move as they separate from each other in mitosis.
spi'reme. A thread formed by the end-to-end union of the chromosomes, found in the mitotic prophase of plants.
spiril'lum (pl. spirilla). The corkscrew-shaped bacterium.
splanch'nic. Concerned with the viscera, layer of mesoderm closely attached to the endoderm.
spleen. A vertebrate organ probably concerned with the growth and destruction of blood corpuscles.
spon'gin. Material found in the skeleton of the common sponge.
sporan'gium (pl. sporangia). The organ in which spores are produced. Contrast gametangium.
spore. An asexual germ cell from which a new individual arises without syngamy. Contrast gamete.
spo'rocyst. A larval stage of the liver fluke.
sporog'enous. Spore-producing.
spo'rophore. A structure on which spore-producing elements are borne.
spo'rophyll. A leaf on which sporangia are borne.
spo'rophyte. The asexual generation of plants with alternation of generations. Contrast gametophyte.
sporula'tion. The act of producing spores.
sta'men. The organ of the flower which produces pollen; microsporophyll.
stape'dial. Having to do with the stapes, a bone in the middle ear.
steppe. Grasslands in cold and dry climates.
ster'num (pl. sterna). The breast-bone of vertebrates.
stig'ma (pl. stigmata). Extended end of the stele secreting a fluid to which pollen adheres and germinates.
stim'ulus (pl. stimuli). A change in the environment which produces a response in protoplasm.
sto'ma (pl. stomata). An opening in the epidermis of the leaf between two guard cells.
stomodae'um (pl. stomodaea). An inpushing of ectoderm in the vertebrate embryo from which the mouth develops.
strobi'lus. A spore-forming organ of gymnosperms; e.g., the pine-cone.
style. Stalk arising from the ovary of the pistil terminating in the stigma.
submuco'sa. A layer of tissue of the vertebrate digestive tube next to the mucosa.
suspen'sor. Cell bodies by which the embryo seed plant is attached to the placenta.
sym'biont. One of two species associated in what appears to be a mutually advantageous partnership.
sympathet'ic. *See* autonomic.
syn'apse. Contact between the processes of two nervous cells.
synap'sis. Temporary union of chromosomes one of which is paternal and the other maternal in origin during the maturation of the germ cells.
syncyt'ium (pl. syncytia). A mass of protoplasm containing a number of nuclei.
synecol'ogy. The study of the biotic community.
syner'gid. Nucleus of the embryo sac at the end away from the placenta in seed plants.
syn'gamy. The union of two gametes by which a zygote is formed.
syno'vial. Having to do with the joints between bones in vertebrates.

T

tac'tile. Associated with the sense of touch.
tar'sal. Having to do with the ankle.
taxon'omy. The study of classification.
tel'ophase. The last stage of mitosis.
tel'son. A tail-like appendage of crustacea.
ten'don. A tough tissue by which a muscle is attached to the bone.
ter'gum. A segment of exoskeleton covering one of the abdominal segments of crustacea.
tes'tis (pl. testes). The male sex gland in animals.
tet'rad. A chromosome with four parts produced by the synapsis of two chromosomes each of which is divided in two parts.
tet'raploid. Having four haploid sets of chromosomes.
thal'lus. A plant body without leaves, characteristic of multicellular algae.
thy'mus. An endocrine gland located near the pharyngeal of vertebrates.
thy'reoid. An endocrine gland also in the pharyngeal region of vertebrates which secretes thyroxin.
thyrox'in. The endocrine secreted by the thyreoid gland containing iodine and increasing the basal rate of metabolism.
tib'ia (pl. tibiae). One of the two shin bones of vertebrates. *See* fibula.
tibia'le (pl. tibialia). The tarsal bone articulating with the tibia.
tibiofib'ula (pl. tibiofibulae). Bone arising from the fusion of the tibia and fibula, as in the frog.
til'lering. The act of branching below ground, thus causing the development of several shoots from the same root, as in wheat.
tis'sue. An aggregate of similar cells.
to'nus. Degree of tension exhibited by muscles.
trabec'ula (pl. trabeculae). A small beam, hence applied to bony bridges seen in the head of the femur, etc.
tra'chea (pl. tracheae). Tube leading from the pharynx to the lungs in vertebrates.
tra'cheid. Elongated cell which conducts water from the vascular bundles in some of the higher plants.
transpira'tion. The evaporation of water from plant leaves, thus pulling absorbed water up from the roots.
trich'ocyst. Thread-like structure which may be expelled from the cell.
trip'loid. Having three haploid sets of chromosomes.
trop'ism. Change in the direction of growth or movement in response to stimulus.
tun'dra. Arctic vegetation area.
tur'gor. Pressure exerted outwards against the wall of the cell when placed in a hypotonic solution.
tym'panum (pl. tympana). The ear drum.

U

ure'a. Waste product containing nitrogen, excreted by the kidneys.
ure'ter. Duct from the kidney leading to the urinary bladder or cloaca in vertebrates.
urogen'ital. Pertaining to the excretory and reproductive systems.
u'terus. Dilated region of the oviduct.

V

vac'uole. Cavity of the cell filled with liquid.
vas'cular. Conducting.
veins. Vessel in which the blood is carried toward the heart.
vent. Aperture of the cloaca.
ven'tral. On the lower or belly side. Contrast dorsal.
ven'tricle. Chamber of the heart with muscular walls by whose contraction the blood is forced into the arteries.
ver'tebra (pl. vertebrae). One of the backbones.
ves'icle. A bladder-like structure.

vi'rus. A disease-causing matter.
vis'cus (pl. viscera). One of the organs found in a cavity of the body, particularly the abdominal cavity.
vi'tamine. Organic substance of unknown chemical constitution but an essential element in animal nutrition.
vitel'line. Having to do with the yolk, especially applied to a thin membrane surrounding the egg.

X

X-chro'mosome. A type of chromosome of which the female usually possesses two and the male one.
xan'thophyll. A yellow pigment found in chromoplasts and chloroplasts.
xy'lem. Vascular tissue through which the sap ascends; contrast phloem.

Y

Y-chro'mosome. The synaptic mate of the X-chromosome found in the males of some species.

Z

zoe'a. Larval form of some crustacea.
zoöl'ogy. Study of animals.
zo'öspore. Asexual motile spore.
zy'gospore. Fused gametes in a protective cyst, corresponding to a zygote.
zy'gote. Fused gametes: fertilized egg.

APPENDIX II

CLASSIFICATION OF ORGANISMS[1]

KINGDOM PLANTAE

Phylum I. Thallophyta: plants without differentiated roots, stems and leaves (60,000 species).

Subphylum A. Algae: holophytic thallophytes.

Class 1. Cyanophyceae: blue-green algae. *Oscillatoria*, etc. (Fig. 151).
Class 2. Chlorophyceae: green algae. *Oedogonium* (Fig. 97), *Ulothrix* (Fig. 96), *Spirogyra* (Fig. 152).
Class 3. Phaeophyceae: brown algae. *Fucus* (Fig. 153), *Postelsia* (Fig. 134), *Sargassum*.
Class 4. Rhodophyceae: red algae. *Pterosiphonia* (Fig. 154).

Subphylum B. Fungi: saprophytic or parasitic thallophytes.

Class 5. Schizomycetes: bacteria. *Clostridium*, *Azotobacter*, *Nitrosomonas*, *Nitrobacter*, *Bacillus* (Figs. 155, 156, 157).
Class 6. Myxomycetes: slime molds[2] *Comatricha*, etc. (Fig. 158).
Class 7. Phycomycetes: molds with syncytial mycelia. *Saprolegnia* (Figs. 160, 161).
Class 8. Ascomycetes: fungi which produce asexual ascospores, yeasts (Fig. 93), molds with multicellular mycelia, the fungal member of lichens (Fig. 161), etc.
Class 9. Basidiomycetes: fungi whose spores are produced by basidia, rusts, mushrooms (Fig. 162), etc.

Phylum II. Bryophyta: multicellular holophytic plants with alternation of generations in which the sporophyte generation is parasitic on the gametophyte. Mostly terrestrial and with some differentiation of organs. (8000 species.)

Class 1. Hepaticae: liverworts. *Riccia* (Fig. 163).
Class 2. Musci: mosses. *Funaria* (Fig. 100).

Phylum III. Pteridophyta: vascular plants with alternation of generations in which both generations are holophytic. Mostly terrestrial and with differentiated organs for absorption and photosynthesis. (6000 species.)

Class 1. Filicineae: ferns. *Pteris* (Fig. 164).
Class 2. Equisitineae: horsetail rushes. *Equisetum* (Fig. 165).
Class 3. Lycopodineae: club-mosses. *Selaginella* (Fig. 168).

Phylum IV. Spermatophyta: seed plants with alternation of generations in which the gametophyte is parasitic upon the sporophyte. (120,000 species.)

Subphylum A. Gymnospermae: spermatophytes in which the seed is not concealed in an ovary.

Class 1. Cycadales: fern-like gymnosperms. *Cycas* (Fig. 149).
Class 2. Gingkoales: *Gingko*.
Class 3. Coniferales: pines, etc. *Pinus*.

[1] Groups now extinct are not included. Some 12,000 extinct species of plants are recognized, and at least 50,000 species of animals.
[2] This group is often included in the class Sarcodina, Phylum Protozoa (page 262).

Subphylum B. Angiospermae: spermatophytes in which the seed is concealed in an ovary; flowering plants.

Class 4. Monocotyledoneae: embryo with one cotyledon, vascular bundles scattered, flower parts reduced. *Triticum* (Fig. 34).
Class 5. Dicotyledoneae: embryo with two cotyledons, vascular bundles forming a ring in stem. *Pisum*, *Sequoia*, etc.

KINGDOM ANIMALIA

Phylum I. Protozoa: unicellular animals (10,000 species).

Class 1. Flagellata: flagellate protozoa. *Euglena* (Fig. 64), *Pleodorina* (Fig. 70), *Volvox* (Fig. 71), *Trypanosoma* (Fig. 170).
Class 2. Sarcodina: protozoa which form pseudopodia. *Amoeba* (Fig. 72), *Endamoeba* (Fig. 170), *Polystomella* (Fig. 170).
Class 3. Infusoria: protozoa with cilia at some stage in the life history and usually with meganuclei and micronuclei. *Paramecium* (Fig. 67), *Carchesium* (Figs. 80, 170).
Class 4. Sporozoa: protozoa without motile organs and reproducing by sporulation. *Monocystis* (Fig. 94), *Plasmodium* (Fig. 122).

Phylum II. Porifera: sessile marine or fresh-water multicellular animals with two germ layers only. (2500 species.)

Class 1. Calcarea: sponges with a skeleton of calcareous spicules. *Grantia.*
Class 2. Hexactinellida: sponges with a skeleton of siliceous spicules. *Euplectella.*
Class 3. Demospongia: sponges with a skeleton of spongin, *Spongilla* (Fig. 171).

Phylum III. Coelenterata: attached or free-swimming marine (rarely fresh-water) multicellular two-layered animals with a single body cavity (coelenteron) opening to the exterior by a single orifice (5000 species).

Class 1. Hydrozoa: hydroids and medusae without mesenteries. *Hydra* (Figs. 76, 95), *Obelia* (Fig. 101).
Class 2. Scyphozoa: exclusively marine hydroid generation small and with mesenteries, medusoid generation without velum. *Aurelia* (Fig. 172).
Class 3. Anthozoa: Marine forms without a medusoid generation. Corals, etc. (Fig. 173).

Phylum IV. Platyhelminthes: Flatworms, without a coelom and anus (5000 species).

Class 1. Turbellaria: Free-living aquatic or terrestrial forms. *Planaria.*
Class 2. Trematoda: Parasitic flatworms with mouth at anterior end. *Fasciola* (Fig. 174).
Class 3. Cestoda: Tapeworms, with an attaching scolex and series of metameric and detachable proglottids. *Taenia* (Fig. 175).

Phylum V. Nemathelminthes: Roundworms, unsegmented and coelomate (100,000 species). *Trichinella* (Fig. 176), *Necator.*

Phylum VI. Echinodermata: Coelomate animals with a spiny exoskeleton and a pentaradial symmetry. (5000 species.)

Class 1. Asteroidea: starfish, *Asterias* (Fig. 178).
Class 2. Ophiuroidea: brittle stars.
Class 3. Echinoidea: sea-urchins, *Arbacia.*
Class 4. Holothuroidea: sea-cucumbers, *Thyone.*
Class 5. Crinoidea: sea-lilies, *Metacrinus.*

Phylum VII. Annelida: segmented worms (5000 species).

Class 1. Archiannelida: marine forms with indistinct metamerism and without setae. *Polygordius* (Fig. 181).
Class 2. Chaetopoda: fresh-water, marine and terrestrial forms with setae. *Nereis* (Fig. 181), *Lumbricus* (Fig. 180).
Class 3. Hirudinea: leeches (Fig. 181).

Phylum VIII. Mollusca: unsegmented coelomate animals usually with a protective calcareous exoskeleton. (60,000 species.)

Class 1. Amphineura: Bilateral flattened molluscs with or without a series of calcareous plates. *Chiton* (Fig. 183).
Class 2. Gastropoda: Asymmetrical molluscs usually with a coiled shell. Snails, etc. *Helix* (Fig. 183).
Class 3. Scaphopoda: Bilateral molluscs with a cylindrical shell. *Dentalium* (Fig. 183).
Class 4. Pelecypoda: Molluscs with a bivalved shell. Oyster, clams, etc. *Anadonta* (Figs. 182, 183).
Class 5. Cephalopoda: Molluscs with long tentacles surrounding the mouth. *Octopus* (Fig. 183).

Phylum IX. Arthropoda: segmented coelomate animals with segmented appendages and a chitinous exoskeleton (400,000 species described; 2,000,000 estimated).

Class 1. Crustacea: Gill-breathing arthropods with two pairs of antennae. *Astacus* (Fig. 185), *Homarus*, *Daphnia* (Fig. 131), *Sacculina* (Fig. 121).
Class 2. Onychophora: One pair of antennae, tracheal breathing, and many pairs of legs. *Peripatus* (Fig. 185).
Class 3. Myriapoda: centipedes and millipedes (Fig. 185).
Class 4. Insecta: six-legged arthropods with one pair of antennae and tracheal breathing.
[1] **Order i. Aptera:** wingless insects, *Lepisma* (Fig. 187).
Order ii. Pseudoneuroptera: insects with two pairs of wings, biting mouth-parts and incomplete metamorphosis. May-flies, *Ephemera* (Fig. 187), etc.
Order iii. Orthoptera: insects with two pairs of wings with the outer pair leathery, biting mouth-parts, and incomplete metamorphosis. Grass-hoppers, roaches, *Periplaneta* (Fig. 187), etc.
Order iv. Hemiptera: insects wingless or with two pairs of wings, sucking mouth-parts and incomplete metamorphosis. The bugs (Fig. 187), *Microsiphum*, etc.
Order v. Neuroptera: insects with two pairs of wings, biting mouth-parts and a complete metamorphosis. Dobson-flies (Fig. 187), etc.
Order vi. Lepidoptera: insects with two pairs of wings, sucking mouth-parts and a complete metamorphosis. Butterflies, moths (Fig. 187), etc.
Order vii. Diptera: insects with a single pair of wings, sucking mouth-parts and complete metamorphosis. Mosquitoes, flies (Fig. 187), *Drosophila* (Fig. 111), etc.
Order viii. Coleoptera: insects with two pairs of wings with the outer pair leathery, biting mouth-parts and complete metamorphosis. Beetles (Fig. 187).
Order ix. Hymenoptera: insects with two pairs of wings, biting or sucking mouth-parts, complete metamorphosis. First abdominal segment fused to abdomen. Often social. Bees (Fig. 99), wasps, and ants (Figs. 123 and 187).
Class 5. Arachnida: without antennae, breathing by book gills or book lungs. Spiders (Fig. 185), scorpions, *Limulus*.

Groups of uncertain systematic position. (Fig. 177.)

Ctenophora: Sea combs (100 species). Marine forms sometimes assigned to the Coelenterates.

[1] These groups are broken up by entomologists into about 25 orders which the limits of this text forbid even enumerating.

Mesozoa: A very few simple or degenerate forms most of which are considered parasitic Platyhelminthes.

Acanthocephala: Parasitic worms with spiny processes on the anterior end sometimes considered Nemathelminthes (100 species).

Chaetognatha: Small marine carnivorous worms sometimes placed with the Nemathelminthes (30 species).

Nemertini: ciliated free-living roundworms sometimes placed near the Platyhelminthes (100 species).

Nematomorpha: long hair-like roundworms whose larvae are parasitic. Usually placed with the Nemathelminthes (20 species).

Rotifera: microscopic metazoa with ciliated disks at anterior end (1000 species). Often made an independent phylum.

Bryozoa: minute colonial forms with ciliated tentacles (1800 species). Sometimes classed with the next two groups as a phylum (Molluscoidea).

Phoronidea: Marine sessile worm-like forms with tentacles, etc., resembling Bryozoa (10 species).

Brachipoda: Marine mollusc-like forms with bivalve shell and internal processes bearing tentacles like two preceding groups (150 species).

Gephyrea: unsegmented marine worms with an anterior protrusible introvert. Sometimes placed near the Annelida (100 species).

Phylum X. Chordata: coelomate animals possessing at some time in the life history a notochord, visceral clefts, and with a dorsal nervous system (60,000 species).

Subphylum A. Hemichordata: worm-like marine chordates. *Balanoglossus.*

Subphylum B. Urochordata: mollusc-like marine chordates. *Styela.*

Subphylum C. Cephalochordata: fish-like marine chordates. *Amphioxus* (Fig. 188).

Subphylum D. Vertebrata: chordates in which the notochord is supplemented or replaced by a chain of vertebrae.

Class 1. Cyclostomata: fresh-water or marine vertebrates without true jaws or paired appendages and with a cartilaginous skeleton. Lampreys *Petromyzon* (Fig. 189).

Class 2. Chondrichthyes: fresh-water or marine vertebrates with true jaws and paired appendages (fins) and a cartilaginous skeleton. Sharks, rays, dogfish (Fig. 189).

Class 3. Osteichthyes: fresh-water or marine vertebrates with true jaws, paired fins and bony skeleton. All common fish (Fig. 189).

Class 4. Amphibia: fresh-water or terrestrial vertebrates with tetrapod appendages and naked skin. Eggs laid in water. *Rana* (Fig. 7), *Necturus* (Fig. 190), *Amblystoma* (Fig. 82).

Class 5. Reptilia: fresh-water, marine, or terrestrial tetrapod vertebrates with scaley skin. Eggs laid on land or ovo-viviparous. Turtles, snakes, lizards, alligators (Fig. 192).

Class 6. Aves: terrestrial vertebrates in which the anterior pair of appendages are used as wings and the body is covered with feathers. The birds. *Gallus* (Fig. 102).

Class 7. Mammalia: tetrapod vertebrates in which the skin is covered with hair and the offspring is suckled.

Subclass a. Prototheria: Egg-laying mammals. *Ornithorhynchus* (Fig. 193).

Subclass b. Metatheria: Viviparous mammals which carry the young for a time in an abdominal pouch. Opossum, kangaroo (Fig. 193).

Subclass c. Eutheria: Placental mammals.

[2] **Order 1. Insectivora:** Insect eaters. Mole.

Order 2. Chiroptera: Flying insectivores and fruit eaters. Bat.

[2] Like the insects, the mammals are divided into many orders. The classification here given is an obsolete arrangement, adopted to conserve space in an elementary text.

Order 3. Carnivora: Meat-eating eutheria. Cat, dog.
Order 4. Rodentia: Gnawing eutheria. Rat, rabbit.
Order 5. Edentata: Toothless eutheria or those whose teeth lack enamel. Armadillo.
Order 6. Ungulata: Hooved herbivores. Horse, cow, elephant, manatee (Fig. 193).
Order 7. Cetacea: Marine mammals in which the legs are converted into fin-like flippers. Whale.
Order 8. Primates: Arboreal and terrestrial forms which have nails at the ends of the digits. Lemurs, monkeys, apes, and men.

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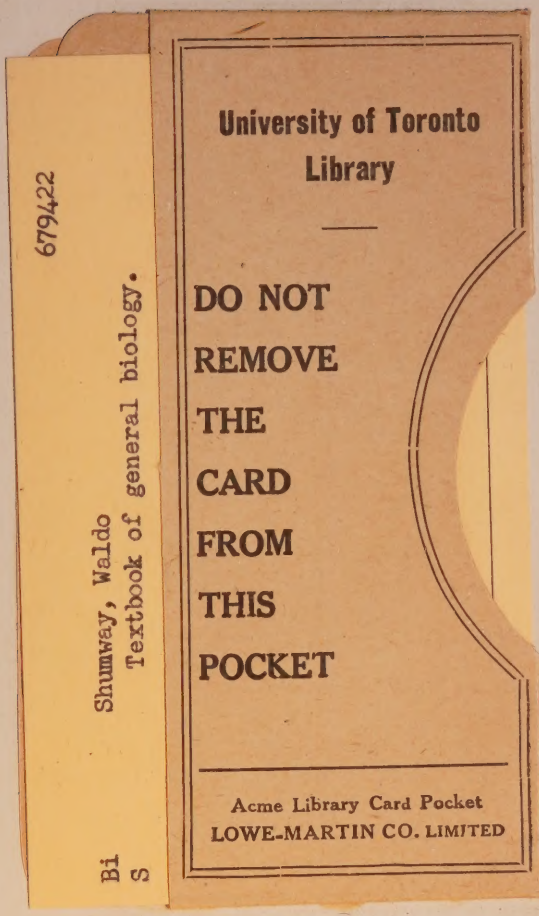

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